University of Alberta

IDENTIFYING HABITATS FOR PERSISTENCE OF GREATER SAGE-GROUSE (*Centrocercus urophasianus*) IN ALBERTA, CANADA

by

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Abstract

Greater sage-grouse (*Centrocercus urophasianus*) currently occupy half of their historic range and populations range-wide have declined by 15-90%. The endangered Alberta population has declined by as much as 92%, likely a result of reduced recruitment due to low nest success and poor chick survival. I use spatial modelling techniques to understand various habitat, climatic, and anthropogenic factors that drive nest and brood habitat selection, and concurrently assess factors that make habitats 'risky' for nests and chicks. At local scales, females recognised ecological cues related to nest success, selecting for large dense patches of sagebrush with thick grass cover, placing their nests under moderate density shrubs with suitable obstruction cover from tall grass. Enhanced nest success resulting from forb cover at all scales, and additional shrub species at larger scales, however, are ecological cues that are missed, potentially creating ecological traps. Broods used habitats that were rich in forbs and had moderate sagebrush cover, tall grass, but less grass cover. Although selection for sagebrush enhanced chick survival, avoidance of grass dominated areas increased risk. Sage-grouse may be making tradeoffs between secure-dense cover habitats, and rare forb-rich foraging habitats that are more open and inherently more risky, particularly in dry years. Landscape-scale models showed selection for heterogeneous patches of high sagebrush cover and strong avoidance of anthropogenic edge habitat for nest sites. Similar heterogeneous high productivity habitats with sagebrush are selected by broods while avoiding human developments, cropland, and high densities of oil well sites. Chick failure tended to occur in proximity to oil and gas developments and along riparian habitats. I predicted these models spatially, identifying source habitats where nests or chicks were likely to occur and survive, and ‘attractive’ sink habitats where occurrence is high, but nests fail and chicks die. Ten percent and 5% of the study area was source habitat, whereas 19% and 15% of habitat was sink habitat for nest and broods, respectively. My habitat models identified areas that need protection, and habitats that need immediate management to enhance recruitment and sustain the viability of this population. I make management recommendations following a collaborative adaptive management approach.

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Chapter One

General Thesis Introduction

Greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') have been studied for over 100 years, with early research focusing on the lek mating system and behavioural questions (Bond 1900; Scott 1942; Patterson 1952; Eng 1961; Eng 1963). As the 1970s approached, a shift in research to more applied research management questions began, addressing population estimation and lek attendance (Dalke et al. 1963; Jenni and Hartzler 1978; Emmons and Braun 1984), hunter harvests (Braun 1979; Braun 1984; Braun and Beck 1985), and habitat requirements (Klebenow and Gray 1968; Eng and Schladweiler 1972; Wallestad 1975; Connelly et al. 1981). This culminated in the development of management guidelines for the maintenance of sage-grouse habitats (Braun et al. 1977), later revised in 2000 (Connelly et al. 2000). Combined with observed population declines (Dalke et al. 1963; Connelly and Braun 1997; Braun 1998), this information resulted in significant research on sage-grouse habitat requirements (Dunn and Braun 1986; Gregg et al. 1994; Fischer et al. 1996; Aldridge and Brigham 2002; Knick et al. 2003), population dynamics across various life stages (Connelly et al. 1993; Schroeder 1997; Johnson and Braun 1999; Aldridge and Brigham 2001; Zablan et al. 2003) and more recently, genetics related research (Young et al. 2000; Benedict et al. 2003; Taylor et al. 2003).

Sage-grouse inhabit shrub-steppe ecosystems, which have undergone major changes during the past 100 years, resulting in habitat loss, fragmentation, and degradation (Knick et al. 2003; Connelly et al. 2004). As a result, sage-grouse currently occupy half of their historic range (Schroeder et al. 2004) and all populations have declined, ranging between 15-90% (Connelly and Braun 1997; Braun 1998; Connelly et al. 2004). Today, the abundance and quality of remaining habitats are threatened by a diverse suite of influences, including conversion of native habitats to agriculture (Connelly et al. 2004), invasion of habitats by non-native plant species (Knick et al. 2003; Connelly et al. 2004), energy extraction activities and developments (Braun et al. 2002; Lyon and Anderson 2003), intense grazing pressures (Beck and Mitchell 2000; Hayes and Holl 2003; Crawford et al. 2004), and even global climate change (Thomas et al. 2004).

The relationship between patterns of grazing, energy developments, human infrastructure (roads, rural encroachment, etc.) and sage-grouse habitat requirements, have important management ramifications. Threshold responses across various life-history stages can greatly assist management of these habitats for viable populations of sage-grouse, particularly in light of the unpredictable threat that West Nile virus (Naugle et al. 2004) poses to small populations. Given that population declines have been linked to poor nesting success (Schroeder et al. 1999; Aldridge and Brigham 2001; Connelly et al. 2004) and low chick survival (Aldridge 2001; Burkepile et al. 2002), management aimed at improving habitat quality for nesting and brood rearing are likely to have the greatest benefits for declining populations.

Species-habitat relationships have become an increasing priority in the field of conservation biology (Boyce and McDonald 1999; Morrison 2001; Brotons et al. 2004; Engler et al. 2004). Simply predicting the occurrence of animals across habitats can be useful, but only if occurrence (or abundance) is somehow positively correlated with fitness (Tyre et al. 2001; Breininger and Carter 2003; Bock and Jones 2004). I define high-quality habitats to be those where animals are likely to occur (high abundance) but also have high fitness (reproduction and survival; Van Horne 1983; Morrison 2001). Conservation biology still struggles to make this crucial link between resources and fitness (Franklin et al. 2000; Morrison 2001; Bock and Jones 2004; Larson et al. 2004; Nielsen et al. 2005), often only addressing where animals occur. Wildlife-habitat management and research should assess both occurrence and fitness. Although much research on sage-grouse has focused on habitat occurrence relationships, or habitat-survival relationships (primarily for sage-grouse nesting habitat), limited work has described how resources influence both occurrence and fitness across multiple life stages.

Based on trends within their currently occupied range, the Alberta sage-grouse population has declined 66-92% since the 1970s (Aldridge and Brigham 2001, 2003). Between 400 to 600 birds remain in the population, which is classified as endangered both provincially and federally (Aldridge and Brigham 2003). While agricultural expansion in the 1970s appears to have isolated Alberta sage-grouse from more southern populations (Aldridge and Brigham 2003), the current landscape is heavily fragmented by roads, power lines, and associated oil and gas activities (Braun, et al. 2002; Aldridge and Brigham 2003). All habitat occurs within the xeric dry mixedgrasss ecosystem and grazing is the dominant land use practice (Adams et al. 2004). An increased frequency of extended drought conditions (Aldridge and Brigham 2002) and the introduction of West Nile virus (Naugle et al. 2004) pose additional threats to the viability of this endangered population. Similar to other populations of sage-grouse, reduced recruitment due to low nest success and poor chick survival has been identified as limiting for this population

(Aldridge and Brigham 2001; 2002; 2003) and long-term habitat management initiatives may be required to improve recruitment and ensure populations remain viable.

The goal of this thesis was to develop models to provide land managers with tools to identify habitats where sage-grouse are abundant and have high fitness (source habitats; Pulliam 1988; Hobbs and Hanley 1990; Breininger et al. 1998), as well as identify habitats in which birds are also likely to occur, but have poor fitness ('attractive sink' habitats; Delibes et al. 2001; Breininger and Carter 2003; Larson et al. 2004). I used empirical models to understand occurrence and fitness-habitat relationships for sage-grouse in Alberta. I assessed these habitat relationships from 2001-2004 in a core use area (1,100 km^2) within the 4,000 km^2 range of sage-grouse in southeastern Alberta. I developed models at various local and landscape scales for nests and chicks, the two most critical life stages for sage-grouse (Aldridge 2001; Crawford et al. 2004). I used resource selection functions (RSFs; Manly et al. 2002) to develop occurrence models and I used Cox proportional hazards models (Cox 1972; Andersen and Gill 1982) to develop survival models. Depending on the scale, life stage, and model type, I considered a variety of different habitat, climate, and anthropogenic variables for inclusion in each model. With the exception of the chick survival models, I had an independent set of data collected within this same study area from 1998-2000, which I used to validate all models and assess model predictive capacity.

In chapter 2, I modeled nest occurrence using local vegetation characteristics selected by females (4th order; Johnson 1980) at three scales surrounding the nest site. I developed survival models using local vegetation characteristics that best predict nest failure/survival at each scale. In chapter 3, I took a similar approach, assessing 4th order habitat selection by sage-grouse broods and chick survival using habitat variables as well as several climate covariates. In that chapter, I also introduced the use of shared-frailty proportional-hazards models (Therneau et al. 2003; Wintrebert et al. 2005) to account for a lack of independence of chicks within broods, and compared these models to more traditional 'brood' survival and chick flush count methods. In both chapter 2 and 3, I used these models to identify vegetation thresholds, above which sage-grouse are likely to be successful.

In chapter 4, I used similar modeling approaches, but used a Geographic Information System (GIS) to model landscape scale habitat and anthropogenic features linked to both nest and brood occurrence and nest and chick survival. I used these models to identify various habitat states, depicting habitats which are likely to be 'sources' and in need of protection, and habitats which are likely to be 'attractive' sinks resulting in ecological traps (Bock and Jones 2004; Battin 2004) that will require management. Finally, I evaluated the effectiveness of current sage-grouse habitat management initiatives, using the recommended 3.2-km habitat-protection buffer around lek sites (Connelly et al. 2000) and the 1-km protection buffer currently employed within the province of Alberta.

In chapter 5, I discuss recent failures to implement collaborative adaptive management strategies for the Alberta sage-grouse population and a population of sharp-tailed grouse (*Tympanuchus phasianellus*) in Manitoba, highlighting the challenges that lie ahead. That chapter was recently published in the *Wildlife Society Bulletin* (Aldridge et al. 2004). Finally, in chapter 6, I summarise all of my findings, bringing together these results within the context of management requirements for sage-grouse in general, and more specifically, within the context of the Alberta population.

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Chapter Two

Predicting Greater Sage-Grouse Nest Occurrence and Survival in Southeastern Alberta: a Fine Scale Approach

1. Introduction

Understanding species-habitat relationships, and thus, predicting species occurrence or density has become an increasing priority in the field of conservation biology (Boyce and McDonald 1999; Morrison 2001; Brotons et al. 2004; Engler et al. 2004; Nielsen et al. 2005), particularly for threatened and endangered species. Occurrence is often thought of as a surrogate measure of habitat quality. In 1983, van Horne proposed that habitat quality should be defined as the product of density (probability of occurrence), survival probability, and expectation of future offspring (fecundity), or what she referred to as "mean individual fitness per unit area". Thus, 'habitat quality' assessments based on occurrence alone are missing the crucial link to survival or overall fitness (Van Horne 1983; Tyre et al. 2001; Breininger and Carter 2003) and have been shown to be a poor indicator of survival (Van Horne 1983; Hobbs and Hanley 1990; Tyre et al. 2001). Despite the passing of more than 20 years of conservation and wildlife science since van Horne's (1983) seminal discussion of how, and what, constitutes good measures of 'habitat quality', the field of ecology is still struggling to make the link between resources and fitness (Franklin et al. 2000; Morrison 2001; Bock and Jones 2004; Larson et al. 2004; Nielsen et al. 2005).

Occurrence or density estimates often lack information about the mechanisms of habitat selection and quality, are unlinked to fitness measures, and ultimately, may be uninformative about population persistence. As Morrison (2001) clearly pointed out in his review on the limits of wildlife-habitat relationships; "we repeatedly fail to find commonalities in 'habitat' for most populations across space because we usually miss the underlying mechanisms…determining occupancy, survival and fecundity." He further noted that the surrogates that we continually use are simply 'hit-and-miss' attempts to statistically model wildlife-habitat relationships (Morrison 2001). Including fitness measures in habitat modeling is of paramount importance for conservation of threatened and endangered species. Without the link between occurrence and fitness, surrogate 'habitat quality' models using occurrence only, could naively result in the implementation of inappropriate management strategies.

Suitable measures of fitness for many wildlife species are often difficult to obtain, due to the long-lived nature of those species. Sample sizes are often an issue when working with rare or endangered species, limiting our ability to understand variability around those parameters. Nonetheless, one should still strive to find measures of fecundity and survival that link to species' resource needs and ensure population viability, the ultimate goal of conservation biology. Spatially explicit habitat-based population-viability analysis linking resources to population demographics has proven to be a promising tool for understanding animal-habitat relationships, whether modelling finer scale mechanisms (Franklin et al. 2000; Johnson et al. 2001) or large scale surrogates in a Geographic Information System (Akcakaya and Atwood 1997; Boyce and McDonald 1999; Larson et al. 2004).

The key to managing habitats for endangered species is 1) that habitats available to the species have a high likelihood of being encountered, assessed and ultimately used, and 2) that animals are successful (survive and reproduce) in their use of those habitats. Thus, maintaining high quality habitats might not result in viable populations if animals do not recognize the habitats as such, and instead, choose to occupy poorer quality habitats. This can result in ecological traps, which may be naturally occurring or a result of human alteration of resources and landscapes (Donovan and Thompson 2001; Bock and Jones 2004). Thus, assessing fitness alone also may result in management actions to which animals cannot respond. Rather, one must understand both occurrence and fitness as they relate to resources when assessing habitat quality or managing to ensure rare or endangered populations remain viable. From a management perspective, making the link between resources and fitness will ultimately result in informed management decisions that have the greatest chance of achieving management goals, such as long-term population persistence.

Greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') once occupied approximately 1.25 million km^2 of habitat throughout the Great Plains and Intermountain west (Schroeder et al. 2004). Currently, sage-grouse exist in just less than half of that 'historic' range (Schroeder et al. 2004), with an estimated breeding population of 150,000-200,000 birds remaining (Connelly and Braun 1997; Connelly et al. 2004). Individual populations have declined by roughly 15-90% since the early 1970s (Connelly and Braun 1997; Connelly et al. 2004), with an estimated 45-80% decline since the 1950s (Braun 1998). The most severe decline may be at the northern fringe of the species' range, with the Alberta and Saskatchewan populations experiencing a 66-92% decline over the last 30 years (Aldridge and Brigham 2001; Aldridge and Brigham 2002) and a 90% reduction in distribution (Aldridge and Brigham 2003).

Population declines throughout North America appear to be linked to poor productivity as a result of low nesting success (Gregg et al. 1994; Sveum et al. 1998b; Watters et al. 2002; Aldridge and Brigham 2002) and poor recruitment (Johnson and Braun 1999; Schroeder et al. 1999; Aldridge and Brigham 2001; Aldridge and Brigham 2002; Connelly et al. 2004). Many of these studies have focused on fine scale resources to assess habitat quality for sage-grouse, either through comparing use sites to random locations (occurrence), by assessing nest success (fitness) related to resources, or by demographic modelling. At nesting sites, sage-grouse generally select for greater sagebrush cover with more dense herbaceous understory cover (Klebenow 1969; Schroeder et al. 1999; Aldridge and Brigham 2002). Only one study has addressed 4th-order (within patch) selection (Johnson 1980) at scales outside of the nest site itself. Aldridge and Brigham (2002) found evidence that sage-grouse in Alberta were selecting for greater sagebrush not only at the nest site, but surrounding the nest as well. In terms of nest survival, cover and height of grass has been shown to be positively correlated with nest success for both artificial and natural sage-grouse nests (Gregg et al. 1994; Sveum et al. 1998b; Aldridge and Brigham 2002; Watters et al. 2002). Reduced availability of suitable sagebrush cover also can limit nest success (Wallestad and Pyrah 1974; Connelly et al. 1991; Sveum et al. 1998b; Aldridge and Brigham 2002). Thus, external factors reducing cover and height of either herbaceous understory or sagebrush canopy could conceivably lower sage-grouse nesting success. Few studies, however, have addressed both occurrence and fitness, and none have developed predictive multivariate-models assessing habitat selection linked with fitness to understand resource thresholds required to ensure sage-grouse nests successfully hatch; a necessary but lacking tool for the management of sage-grouse nesting habitat.

In this paper, I present the first attempt (to my knowledge) to merge predictive occurrence models with fitness models for greater sage-grouse. I illustrate this process by modelling 4th-order nest occurrence and nest survival, at three different hierarchical scales. Meyer et al. (1998) found that various measures of spotted owl (*Strix occidentalis caurina*) fitness were affected differently, by assessing habitat at increasing concentric radii around nest sites in western Oregon. Similarly, McGrath et al. (2003) found hierarchical selection by northern goshawks (*Accipiter gentilis atricapillus*) for nesting habitat, with different factors influencing selection at different scales. I predict that selection of nesting habitat by sage-grouse is occurring at the nest site, as well possibly at larger radius patch or area scales surrounding the nest. Secondly, if habitat quality varies across the landscape and some variation in selection exists, I expect my survival models to accurately predict nest failure. However, if nest fate (survival model) is driven by characteristics other than those sage-grouse select for (occurrence model), then sage-grouse may be attracted to poor quality habitats (ecological traps) resulting in reduced nest success (a measure of fitness). I also expect that the predictive capability of occurrence and survival models will vary at different hierarchical scales surrounding nest sites, with the best fit models indicating the scale at which selection is taking place or nest failure is driven. Finally, if my models are predictive, I can identify thresholds of habitat quality, providing information where sage-grouse are likely to nest, and where they are likely to be successful. Predictions from these models can be used to direct management actions to ensure the persistence of functional, high-quality nesting habitat for sage-grouse in Alberta.

2. Study area

The study area consisted of a 1,100 km^2 core-use area within the overall 4,000 km^2 sage-grouse range on the dry mixedgrass prairie of southeastern Alberta (49° 24' N, 110° 42' W, *ca* 900 m elevation). The area is composed of diverse plant community types that vary in their productive potential (Adams et al. 2005). Silver sagebrush (*Artemisia cana*) is the dominant shrub and pasture sage (*A. frigida*) the dominant forb. Grasses include needle-and-thread grass (*Stipa comata*), june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*) (Coupland 1961; Aldridge and Brigham 2003).

3. Methods

3.1. Field techniques

I captured females at 5 of 8 known active leks in southeastern Alberta during the breeding season (March through May) from 2001 to 2003 using walk-in traps (Schroeder and Braun 1991) or with a long-handled hoop net and handheld spotlights (Giesen et al. 1982; Aldridge and Brigham 2002). Sex and age [(yearlings <2-years-old) and (adults ≥2-years-old)] of all captured individuals were determined based on shape and length of the outermost primaries of each bird (Eng 1955; Crunden 1963). Each captured female was fitted with a 14-g necklace-style radiotransmitter (RI-2B transmitters; Holohil Systems Ltd.; Carp, ON Canada).

Females were located every second day using a 3-element Yagi antenna and an R-1000 scanning telemetry receiver (Communications Specialists, Inc. Orange, CA). Standard telemetry techniques were used to determine locations of females. Signals were triangulated until birds could be directly observed from approximately 30 m. These locations were recorded in Universal Transverse Mercator coordinates using a hand held 12 Channel Global Positioning System (Garmin 12 XL and GPS II Plus; Garmin International Inc., Olathe, KS). When signals could not be located, I searched the study area from a fixed-winged aircraft.

Date of nest initiation was estimated as the midpoint between the last date when the female did not display localized movements and the first direct observation of the female on a nest (Manolis et al. 2000). Date of nest success or failure was estimated as the midpoint between the last observation of the female on the nest and the first observation of the female off the nest (Manolis et al. 2000). A nest was considered successful if ≥1 egg hatched, as evidenced by detached egg membranes (Klebenow 1969; Aldridge and Brigham 2002). A nest was considered unsuccessful if eggs were broken, or the membranes of egg shells remained intact.

Nest site characteristics were measured similar to previous studies by following the recommendations of Connelly et al. (2000, 2003). To maintain consistency with previous research, I followed methods used by Aldridge and Brigham (2002). I estimated the percent sagebrush canopy cover, percent cover of total grasses (current and previous year's standing growth combined), non-palatable forbs [prickly pear cactus (*Opuntia* spp.), ball cactus (*Coryphantha vivipara*), and moss phlox (*Phlox hoodii*)] which are not common forage items for sage-grouse (Kerwin 1971), forbs [palatable to sage-grouse (see

Kerwin 1971)], shrubs [other than sagebrush; i.e., snowberry (*Symphoricarpos albus*), rose (*Rosa* spp.), greasewood (*Sarcobatus vermiculatus*), and creeping juniper (*Juniperus horizontalis*)], and bare ground/dead materials within a 1-m^2 quadrat. Shrub and understory vegetation were not stratified into separate layers when estimating cover, consistent with Aldridge and Brigham (2002). Therefore, cover estimates could not exceed 100%. Mean maximum height of vegetation for the above groups was also calculated for each quadrat using measurements of three of the tallest plants. In addition to those variables measured by Aldridge and Brigham (2002), I estimated the percent residual grass cover (growth from the previous year but still standing), separating residual grass cover from 'total' grass cover described above. In some cases I noted that sage-grouse were nesting under sagebrush with limited green vegetation, but that the woody stem of the plants still provided some cover. Thus, I also estimated additional cover provided by the sagebrush stem (i.e., ocular estimates of cover provided by the stem itself, above that provided by the canopy). Finally, I estimated vertical obstruction cover concealing the nest using a Robel pole (Robel et al. 1970).

To identify the scale at which habitat characteristics might be selected, I took measurements at the nest itself (nest site) as well as at 8 additional dependent non-random 1-m^2 quadrats. The additional quadrats were placed 7.5- and 15-m (4 each) from the nest site in each of the 4 cardinal directions, representing 2 concentric radii scales surrounding the nest. The area enclosed within the 7.5-m 'patch' scale was 177 m^2, and 707 m^2 within the 15-m 'area' scale, although I analysed each doughnut separately (each 4 quadrats alone), exclusive of data collected at the inner scales. These radii were not biologically determined, but for consistency, followed methods used by Aldridge and Brigham (2002), and have been shown to be relevant to sage-grouse.

To understand sage-grouse selection of sagebrush at nest locations, I also performed additional vegetation measurements on sagebrush along 4-, 15-m transects radiating from the nest site in each cardinal direction. I used a similar method to Canfield's (1941) line intercept method, which may be a more accurate measure of shrub (sagebrush) canopy cover. Aldridge and Brigham (2002) showed that these 2 methods were highly correlated, but that the quadrat method resulted in slightly higher estimates of sagebrush cover. I also estimated the density of sagebrush by counting the number of plants within 0.5 m on either side of the transect (Aldridge and Brigham 2002). Measurements were recorded separately for the first (0-7.5 m) and second (7.5-15 m) halves of the transect corresponding with the scales measured with quadrats. Sagebrush cover was also estimated for the 2, 1-m segments of the line intercept that intersected the center 1-m^2 quadrat over the nest site. Nest concealment cover was estimated at the nest site by averaging four measurements (based on 2-cm height increments) taken with a Robel pole looking towards the nest from 1 m away in each cardinal direction. I estimated concealment cover surrounding the nest by moving the Robel pole further from the nest (2.5-m increments) and averaging measurements over the 1st (2.5-, 5-, and 7.5-m distance) and 2nd halves of each line transect (10-, 12.5-, and 15-m distance), corresponding with the 7.5-m patch and 15-m area radius scales.

Measurements of habitat characteristics were taken at a random location 100 to 500 m from each use site, also using the same protocol for quadrats and line transects, focusing on the random site, patch radius, and area radius scales. Thus, my design was paired, with each use location linked to a single random location, allowing me to better approximate the choices that animals make (Compton et al. 2002). Following Aldridge and Brigham (2002), I chose the random locations by walking between 100 and 500 m (distance randomly chosen) in a random direction from the nest site. The closest sagebrush plant to the random location was used as the "random" nest site, because the majority of nests are placed under sagebrush (Patterson 1952; Klebenow 1969; Connelly et al. 1991; Sveum et al. 1998b; Aldridge and Brigham 2002). When sagebrush cover is sparse, such as that in *A. cana* plant communities, sage-grouse will place their nests under shrubs other than sagebrush (Aldridge and Brigham 2002). If this was the case, random nest locations were located under the closet shrub to the random point. Vegetation characteristics were measured at nest and random locations on the same day, immediately following a successful hatch or a predation event.

3.2. Data Analyses

I evaluated sage-grouse nest occurrence and survival at the 4th-order or local vegetation scale (Johnson 1980). I used a design IV approach, where individuals are identified and followed, allowing the identification of a set of used resources, and availability is uniquely defined for each use point (Erickson et al. 2001). Use sites were compared for survival analyses based on nest fate, and my dependent random locations represented a random sample of unused units that I compared to used units (nests) for occurrence modeling. In no cases were other sage-grouse nests observed at or near the random locations. Thus, I am confident that sage-grouse did not nest at these random sites in that given year, making this random sample an unused sample of resource units.

I conducted all occurrence and survival analyses at three different scales. First, analyses were conducted using only the 1-m^2 quadrat centered on the nest or random unused location to assess survival (use sites only) and occurrence, referred to as the ‘nest site’ scale. I analyzed vegetation characteristics at two concentric radii surrounding the nest site itself using: 1) the ‘patch’ radius scale which included averaged measurements for the 4-quadrats and Robel measurements at the 7.5-m radius (excluding nest site quadrat), as well as the 4, line-transect measurements from 0 – 7.5 m, and 2) the ‘area’ radius scale which included averaged measurements for the 4-quadrats and Robel measurements at the 15-m radius (excluding nest-site and 7.5-m quadrats), as well as the line transect measurements from 7.5 to 15 m only. All analyses were conducted in STATA 8.2 (STATA 2004).

3.2.1. Conditional fixed-effects occurrence analyses

My sampling design using random non-nest locations paired with nest locations is a 1:1 matched case-control design (Hosmer and Lemeshow 2000; Manly et al. 2002), which controls for confounding temporal and spatial factors that can lead to incorrect null models (Compton et al. 2002) and biases in habitat selection (Rosenberg and Mckelvey 1999). Even though I had a sample of used sites (1) and unused sites (0), probabilities generated from the logistic regression models are still relative, due to the conditional nature of my data. Thus, I generated resource selection functions (RSF) for my paired observations using a case-control logistic regression with the following form (Manly et al. 2002:151):

$$\hat{w}(\mathbf{x}_{ij}) = \exp(\hat{\beta}_1 x_{ij1} + \hat{\beta}_2 x_{ij2} + \ldots\ldots + \hat{\beta}_p x_{ijp}) \qquad \text{(2-1),}$$

where $\hat{w}$ is the RSF probability for the *j*th resource unit being selected at the *i*th choice for the predictor variables, x_i, and the $\hat{\beta}_i$'s are the coefficient estimates for each predictor variable. I generated RSFs for all *a priori* candidate models at each scale. For all occurrence models coefficients are presented as unstandardized linear predictor estimates.

3.2.2. Proportional hazards survival analyses

Females were relocated at intervals of ≤2 days during the breeding and nesting period. Thus, I felt comfortable estimating daily nest survival. I was able to locate many nests during laying, but could not be certain of nest initiation dates for all nests, so I chose to model nest survival only during incubation. As a result, three nests that failed prior to the hen incubating were excluded from survival analyses. Nest incubation for sage-grouse in Alberta has been shown to be 27.0 ± 0.6 (SE) days (Aldridge and Brigham 2001), and was 27.5 ± 0.2 (SE) days for 29 nests that successfully hatched at least 1 egg (range 24-29 days) in my study in 2001-2003. Thus, I estimated daily nest survival from initiation of incubation to 28 days (hatch).

I used a Kaplan-Meier product-limit estimator (Kaplan and Meier 1958) with a staggered-entry design (Pollock et al. 1989; Winterstein et al. 2001) to estimate nest survival. In 2002, I had 6 nests that were eventually abandoned by females due to spring snow or rain storms. In all cases eggs had been frozen. I could have chosen to model nest failure as two different competing risks (Lunn and Mcneil 1995) assessing the risk of failure due the different risks (predation or inclement weather). However, given that the majority of nest failures and sage-grouse deaths are a result of predation events (Schroeder and Baydack 2001), and that I only had 6 (of 91) nest failures due to weather, I chose to model nest survival as a function of failure risk due to a nest predation event only. Thus, I considered the six weather-abandoned nests to have successfully avoided a predation event and right censored these observations at the time the female abandoned the nest (Lunn and Mcneil 1995; Winterstein et al. 2001). I used a Log-rank χ^2 statistic to test for differences in survival functions (Winterstein et al. 2001) among years and nest order (1st or 2nd nesting attempts). Given the low proportion of yearlings in the Alberta population (<20 %, Aldridge and Brigham 2001) I did not have the sample sizes to test for age effects on nest survival (2 of 91 nests from radio-collared birds were produced by yearlings).

I used the Cox proportional hazards regression model (Cox 1972; Andersen and Gill 1982; Cleves et al. 2004) to fit nest-survival models with habitat covariates to assess which covariates had the largest impact on nest survival. The Cox proportional hazards model estimates the hazard rate [$h(t|\mathrm{x}_i)$] for an individual ith subject as follows (Cleves et al. 2004):

$$h(t|\mathrm{x}_i) = h_0(t)\exp(\beta_{i1}x_{i1}+\beta_{i2}x_{i2}+\ldots\beta_{in}x_{in}) \qquad (2\text{-}2),$$

where β_i's are the regression coefficients for the x_i variables, and $h_0(t)$ is the baseline hazard that is not parameterized and is left unestimated. Thus, the model makes no assumptions about the hazard over time. I present coefficients for all survival models as hazard ratios ($\exp[\beta_i]$).

I developed Cox proportional hazards models for each of my *a priori* candidate models; all covariates were fixed (i.e., no time varying covariates). I used the Breslow estimation of the continuous-time likelihood calculation to partition deaths with tied failure times (Cleves et al. 2004). The principal assumption when comparing survival functions with the Cox model is that the hazards are proportional over time (Andersen and Gill 1982; Winterstein et al. 2001) or the influence of a treatment or independent variable on the risk of failure does not change over the duration of the study (Cleves et al. 2004). For each of my candidate models, I compared logarithm plots of the estimated cumulative-hazard functions (Andersen and Gill 1982, Cleves et al. 2004) and Schoenfeld residuals (Schoenfeld 1982) to test for violations of the proportional hazards assumption. If logarithm plots with curves of treatment groups are not parallel or plots of Schoenfeld residuals indicate a non-zero slope, the proportional hazards assumption is violated. I used a χ^2 goodness-of-fit test on the Schoenfeld residuals to statistically test for a non-zero slope (Grambsch and Therneau 1994; Cleves et al. 2004). All survival estimates reported are means ± standard errors.

3.2.3. Model development

I initially developed my *a priori* candidate models on data collected from 2001-2003 using the same set of variables that were also collected from 1998-2000 (Aldridge and Brigham 2002). This allowed me to train my candidate models on my current dataset (2001–2003), and validate (test) my models on an independent sample of data (1998–2000; see section 3.2.4 for validation). I then attempted to improve the fit of my models using additional parameters I measured for my current training dataset (2001-2003).

I examined potential collinearity between all predictor variables using Pearson correlations and variance inflation factors (VIF). Collinearity between individual parameters was assumed if correlations were > |0.6| and multicollinearity (Menard 1995) was a concern if individual parameter VIF scores were greater then ten, or the mean VIF score for a given model was considerably larger than one (Chatterjee et al. 2000). I conducted univariate analyses on all predictor variables for both conditional logistic regression occurrence models and Cox survival models to determine which correlated variables to retain (Menard 1995; Hosmer and Lemeshow 2000). Correlated variables that consistently explained greater deviance from the null model (Hosmer and Lemeshow 1999; 2000) across multiple scales for both survival and occurrence models were retained. Studentized and Pearson residuals were inspected for influential outliers with large leverage (Menard 1995; Hosmer and Lemeshow 2000). I visually inspected the data and used the Box-Tidwell transformation for each independent variable to detect if nonlinearities existed in the relationship between each independent variable and the dependent variable [logit (Y)] (Menard 1995; Hosmer and Lemeshow 2000).

Previous research suggested that sage-grouse nest site selection and nest survival is related to canopy cover of shrubs (primarily sagebrush) and tall herbaceous understory cover (see introduction). Thus, each of my candidate models had a shrub component and an herbaceous understory component.

3.2.4. Model selection, assessment and validation

For both survival and occurrence models, I had *a priori* knowledge about which vegetation characteristics were thought to affect nest site selection and success, and thus, chose to take an information-theoretic approach to model selection using Akaike's Information Criteria (AIC) with a correction for small sample size [AIC_c, (Anderson et al. 2000; Burnham and Anderson 2002)]. For the case-control-logistic-occurrence models, the number of paired groups determines the sample size. For the Cox proportional hazards models, essentially a temporal case-control logistic regression approach, sample size is the number of events (Cleves et al. 2004), or in my case, nest failures. For each scale tested, I used the differences in AIC$_c$ scores (Δ_i) to identify the best approximating occurrence or survival model (i.e., most explanatory power) within the candidate set (Anderson et al. 2000; Burnham and Anderson 2002). AIC$_c$ weights (w_i) were used to assess the approximate probability that each model was the best model of the given set (Anderson et al. 2000; Burnham and Anderson 2002).

I assessed the fit of each survival and occurrence model to the data using a likelihood ratio (LR) χ^2 statistic (Hosmer and Lemeshow 2000). As a rough guide to the variance explained for each model (Hosmer and Lemeshow 1999), I estimated the deviance explained (reduction in log-likelihood from the null model). Deviance estimated for survival models are only a relative measure that are heavily influenced by the percentage of censoring (Hosmer and Lemeshow 1999). Thus, direct comparison of these relative measures between my matched case-control logistic occurrence models and proportional hazards survival models may be inappropriate. Comparing the 'relative' deviance estimates between survival models within the same candidate set, however, should be appropriate.

For my occurrence models, I applied the β_i coefficients generated from my top case-controll logistic models to my dataset, predicting relative probabilities of sage-grouse nest occurrence. Probabilities above the an optimal probability cut-off point [point that maximized both the sensitivity and specificity curves (Swets 1988; Nielsen et al. 2004)], were considered as presence and probabilities below the cut-of point were considered as absence. For survival models, I applied the β_i coefficients generated from my top Cox model and predicted the 'relative' nest-hazard rate. Nests with predicted probabilities above the optimal probability cut-off point were predicted to have failed (1) and nest below the cut-off point were considered as survived – reduced hazard (0).

I then assessed the predictive accuracy of all top AIC_c-selected models (occurrence and survival) using receiver operator characteristic (ROC) estimates of the area under the curve (Fielding and Bell 1997). ROC estimates above 0.9 indicate high model accuracy, values between 0.7 to 0.9 indicate good model accuracy, and values between 0.5 to 0.7 were indicative of low model accuracy (Swets 1988; Manel et al. 2001). I also assessed the predictive capacity of the top models at each scale, by estimating the percent correctly classified (PCC) when predicting occurrence or survival and using the optimal cut-off. I considered a PCC of ≥70% to be reasonable model prediction, with a PCC of ≥80% excellent prediction (Nielsen et al. 2004). I assessed the effect of parameters on the top AIC_c-selected survival and occurrence model at each scale using 95% confidence intervals; survival model coefficients that did not overlap 1 (1 = no hazard) contributed to the survival model; occurrence model coefficients that did not overlap zero (0 = no effect) contributed to the occurrence model.

Predicting my proportional hazards models does not take into account the time-to-failure nature of the survival data. Thus, to further assess survival models, I also compared survival functions for all nests classified to have failed (i.e., above optimal cut-off point) and all classified to have survived (i.e., below the cut-point) using a Log-rank χ^2 test. This evaluates the difference in survival curves between nests predicted to fail versus nests predicted to survive. If the model was predictive, survival should be different between the groups, with the failure predicted nests having lower overall survival rates.

Burnham and Anderson (2002:150) suggest that when model uncertainty exists between candidate models (ie., AIC_c weights <0.90) inference on parameters should be made on model averaged coefficients and standard errors. This was difficult, however, given that some of the variables in my candidate model set were combinations of each other (i.e. Bush = sagebrush + shrubs). Model averaging is not however necessary if coefficients are robust across candidate models (Burnham and Anderson 2002:150). Thus, I compared coefficients across my candidate models for stability in predictions as well as biologically interpretable patterns. I also estimated the relative importance of variables by summing the Akaike weights ($\sum w_i$) across all models within the candidate set (Burnham and Anderson 2002). This allowed me to assess the importance of each variable and also compare how effective each sagebrush measurement method (cover quadrats versus line intercept) was at predicting sage-grouse nest occurrence and survival. It also allowed me to test the strength of evidence for a linear versus quadratic response by sage-grouse to sagebrush (see section 4.1 – candidate models).

Once I identified the top AIC_c-selected occurrence and survival models at each scale, I validated these models with an independent sample of 40 nest locations collected from my same study area during 1998-2000 (29 nests from Aldridge and Brigham (2002), and 11 nests from C.L. Aldridge, unpublished data) by predicting occurrence and survival models on this new dataset and assessing fit and prediction as described for model training datasets. Only 38 of the 40 nests from the model testing dataset were used for survival-model validation, as I did not have time-to-event data for two nests produced by unmarked females (unknown date of incubation initiation). Finally, I assessed the relative risk of nest failure across a range of values for each parameter in the model using the coefficient estimates from the top survival-model at each scale. I varied the parameters of interest across 90th percentile of the range of availability for that parameter, while holding all other parameters at their mean values. This allowed me to generate dose-response curves and identify threshold levels for nest survival relative to each parameter of interest. I could not generate similar dose-response curves for my occurrence models due to the conditional nature of the case-control analyses.

4. Results

Over the three years (2001-2003) of my study I located a total of 93 nests produced by 50 different radio-marked individuals (1.8 ± 1.8 nests per individual). Nest survival to hatch (28 days) with weather-failed nests censored on the date the female abandoned the nest was 35.3 ± 5.4% (Figure 2.1). As a more conservative comparison, with those six nests considered as failed, nest survival was 29.6 ± 5.0%. All further analyses are based on the former censored data, focused on nest failure due to predation events only. There was no difference in nest survival between years of my study ($\chi^2_2 = 3.88$, $P = 0.145$). The majority of nests (75/93, 80.6%) were placed at least partially under sagebrush. Of the 91 nests made by radio-marked individuals, 68.8% (64) were initial attempts and 31.2% (29) were renesting attempts. Nest survival to 28 days did not differ between initial (38.4 ± 6.4%) and second nesting attempts (28.0 ± 9.6%, $\chi^2_1 = 0.02$, $P = 0.87$). I had no reason to assume that nest-site selection should change across the years of my study, and thus, I developed candidate models across all years that were independent of first or second nesting attempts (nest order).

4.1. Candidate models

For all scales, sagebrush density estimated along the line transects (SBint) was correlated with % sagebrush cover estimated by the line intercept method (SBint; $r > 0.68$) and sagebrush cover (SB) estimated by ocular estimation with the quadrat method (SB; $r > 0.82$). I dropped sagebrush density for model building. Also, sagebrush cover (SB) and the Canfield line intercept method (SBint) were positively correlated across all scales ($r > 0.68$). Thus, I chose to include both measures of sagebrush cover in competing models (one or the other) to assess the predictive capabilities of each measurement method. In addition, I combined shrub and sagebrush cover estimated from quadrats to derive an overall combined shrub-canopy estimate called 'Bush', which was correlated with both sagebrush cover measures at most scales ($r > 0.65$). I used Bush as a third separate shrub component variable in candidate models.

All vegetation heights were highly correlated with cover estimates for respective vegetation classes across all scales (typically $r > 0.80$, all > 0.63), with the exception grass height and grass cover ($r < 0.55$). I retained grass height as a candidate variable, and for all measurements when no grass was present (i.e., 0% cover), I considered grass height also to be 0, avoiding 'null' data cells and preventing the need to rarefy my dataset. I excluded remaining correlated height variables from my *a priori* candidate models, as they tended to be less predictive than cover estimates (based on deviance). A complete list of variables used in candidate models (shrub and herbaceous groups) is shown in Table 2-1.

In many cases, across measurement types and scales, I found that the relationship between the logit (prediction) and the sagebrush/bush dependent variable was non-linear using the Box-Tidwell transformation. I expected that sage-grouse might select for mid-range cover of sagebrush/shrubs, allowing for a healthy herbaceous understory. Thus, I fit a quadratic relationship for each shrub component variable ($SB + SB^2$, $SBint + SBint^2$, $Bush + Bush^2$), arriving at six different shrub component variables (Table 2-2a). I combined each of these six shrub component variables with six different combinations of the herbaceous component variables (Table 2-2a), to develop 36 different *a priori* candidate models for sage-grouse nest occurrence and survival modeling (Table 2-2b). This allowed me to evaluate shrubs in general versus sagebrush in competing models, and also to assess if a linear versus quadratic relationship better predicted nest occurrence or survival. Thirteen of my 36 candidate models (Table 2-2b) were poorly specified using the Cox proportional hazards approach (χ^2 goodness-of-fit test of non-zero slopes for Schoenfeld residuals, $P < 0.05$), and were excluded as candidate models for both survival and occurrence modeling (see section 4.3 for details).

Visual obstruction cover (Robel), sagebrush stem cover (SBstem), and residual grass cover (Resid) were the three additional parameters I measured from 2001-2003 (Table 2-3a). I re-evaluated the top model at each scale with the addition of these variables added to the top model (six additional model combinations; Table 2-3b). One of the 93 nest sites from my original model training dataset was missing data for these parameters, and thus, only 92 nest pairs were used for occurrence models, but the same 91 nests were used for survival (Table 2-3). Several of the models with SBstem at various scales violated the proportional hazards assumption (χ^2 goodness-of-fit test of the nonzero slopes, $P < 0.05$), and I decided to drop all candidate models with SBstem for survival analyses, but retain SBstem for additional parameter occurrence models.

Residual grass (Resid) was highly correlated with grass cover ($r > 0.77$) at all scales, and was not used in candidate models where the top 2001-2003 AIC$_c$-selected model at that scale contained grass cover (Gr). This was the case only for all occurrence models (Table 2-3b). Thus, additional parameters added to occurrence models were Robel and SBstem, and parameters added to survival models were Robel and Resid (Table 2-3b).

For all tables, due to their small values, I multiplied coefficients, standard errors, and confidence intervals for the Bush^2, SBint^2, Gr, and GrHgt variables by 100 for presentation purposes only. Forb is also multiplied by 100, but for occurrence models only. I refer to non-multiplied values within the text.

4.2. Conditional fixed-effects occurrence analyses

Based on AIC$_c$ weights (w_i), top nest occurrence models did not have strong support (i.e. $w_i > 0.90$) at any of the scales tested for my original 2001-2003 training dataset models (Tables 2-4 to 2-6), and only the nest-site scale showed strong selection for the top additional parameter models (Tables 2-10 to 2-12). At all scales, however, coefficient (β_i) estimates were robust across all models, making inferences about those parameters consistent, regardless of the model used. Thus, I chose not to model average coefficients. Patterns in the coefficients were evident within the groups of top-selected models, which I discuss for each scale.

4.2.1. Nest occurrence at the site scale

All 4 top candidate models at the nest-site scale contained the Bush + Bush^2 parameters (Table 2-4). These four models were predictive, each explaining about 49% of the variation in nest-site selection (Table 2-4). Inferences based on the coefficients from the top model (#16) indicate sage-grouse select strongly for mid-to-high bush cover above the nest (β_{Bush} = 0.156 ± 0.056, β_{Bush2} = – 0.0007 ± 0.0009, concave function, Table 2-7). While there was no discernable selection for grass cover (Gr) at nest sites as the 95% CI confidence intervals overlapped zero (β_{Gr} = 0.0016 ± 0.0021, Table 2-7), there was strong selection for grass that was considerably taller (β_{GrHgt} = 0.048 ± 0.021, Table 2-7). The strength of influence of these parameters is evident from the relative variable importance weightings where the Bush + Bush^2 ($\sum w_i = 0.99$) and GrHgt ($\sum w_i = 0.94$) terms had strong evidence of importance given my candidate set of models (Table 2-8). Note that there was very weak evidence of importance for sagebrush (see all sagebrush variables) unless sagebrush was combined with other shrubs in the Bush + Bush^2 variable (see Table 2-8 below dashed line).

This top AIC$_c$-selected nest site occurrence model (#16) had good fit (LR χ^2_4 = 64.30, $P < 0.001$) and high model accuracy when predicted on both my training and validation datasets (ROC$_{train}$ = 0.929, ROC$_{test}$ = 0.930, Table 2-9). The model also had excellent prediction (85%) for both training and testing datasets (Table 2-9).

The additional parameters model with both Robel and SBstem (model #16-5) was the top AIC$_c$-selected model, had good fit (LR χ^2_6 = 92.77, $P < 0.001$) and strong support ($w_i = 0.90$) within my candidate set of additional parameter models (Table 2-10). Variance explained increased to 73% from the originally selected top AIC$_c$ model (49%; model #16; Table 2-10). Selection for mid-to-high amounts of bush cover above the nest (β_{Bush} = 0.183 ± 0.083, β_{Bush2} = – 0.0018 ± 0.0011) was still strong, and selection for taller grass (β_{GrHgt} = 0.044 ± 0.028) although weaker, was evident (Table 2-13). Strong selection for greater obstruction cover (β_{Robel} = 0.104 ± 0.046) and sagebrush stem cover (β_{SBstem} = 0.266 ± 0.091) explained the increase in deviance. These two variables improved model accuracy when assessed on the training dataset (ROC_{train} = 0.98) and had excellent prediction (PCC_{train} = 92.4%, Table 2-14).

4.2.2. Nest occurrence at the 7.5-m patch radius scale

There was weak support for the top AIC_c-selected model (#36) at the 7.5-m radius scale (w_i = 0.181, Table 2-5). All of the 8 models within the 90% confidence set (i.e. $\sum w_i \geq 0.90$), however, contained the SBint variable, and all but one model contained the GrHgt variable (Table 2-5). All models at the 7.5-m radius scale explained >31% of the variation in nest selection, with the top model (#36) explaining 37% of the variation (Table 2-5). At this patch scale, based on the top model, sage-grouse appear to be more selective for sagebrush as a canopy component than shrubs in general, but females are selecting for mid-to-high range cover ($\beta_{SBint} = 0.792 \pm 0.204$, $\beta_{SBint2} = -0.028 \pm 0.011$, concave function, Table 2-7). Selection was also strong for taller grass cover ($\beta_{GrHgt} = 0.078 \pm 0.037$), with females showing strong avoidance of other (non-palatable) forbs ($\beta_{ForbOth} = \mp 0.350 \pm 0.172$, Table 2-7). Ninety-five percent confidence intervals of β_i estimates for Gr and Forb overlapped zero, indicating neither selection nor avoidance (Table 2-7). The strength of evidence for sagebrush cover estimated by the line intercept method was strong ($\sum w_i = 0.99$) at this scale, with greater evidence for selection of moderate sagebrush cover (i.e., quadratic relationship; $SBint^2$ $\sum w_i = 0.64$) over maximal sagebrush cover (linear relationship; SBint $\sum w_i = 0.36$, Table 2-8). This top AIC_c-selected nest-occurrence model (#36) at the patch scale had good fit (LR $\chi^2_6 = 48.26$, $P < 0.001$), good accuracy (ROC_{train} = 0.873, ROC_{test} = 0.884, Table 2-9), and good prediction (PCC_{train} = 78.5%, PCC_{test} = 82.5%, Table 2-9).

Of the additional parameters models, model #36-1 with the addition of Robel was selected as the top AIC$_c$ model and had good fit (LR $\chi^2_7 = 54.70$, $P < 0.0001$). There was moderate support ($w_i = 0.72$) for this model within my candidate set of additional parameter models, and while the variance explained was better (42.9%), it only increased 6% over the base model (model 36; Table 2-11). Inferences about parameters with the additional Robel variable were similar to the base model (see Table 2-7), with selection remaining strong for mid-to-high ranges of sagebrush cover (Table 2-13). Taller grass cover ($\beta_{Gr} = 0.060 \pm 0.041$), however, was now only weakly selected for and cover of other forbs ($\beta_{ForbOth} = -0.321 \pm 0.173$) was only weakly avoided (Table 2-13). Even at this patch scale (7.5 m from the nest), selection was again strong for greater obstruction cover ($\beta_{Robel} = 0.127 \pm 0.053$, Table 2-13) and this model (#36-1) with Robel had high model accuracy (ROC$_{train}$ = 0.89, Table 2-14) and good fit (PCC$_{train}$ = 80.4%; Table 2-14), similar to the original base model (Table 2-9).

4.2.3. Nest occurrence at the 15-m radius scale

The top AIC$_c$-selected model (#25) at the 15-m radius area scale had very little support, ($w_i = 0.173$, Table 2-6). This model contained only the SBint and Gr variables, and had similar weight to the second ranked model (#27; $w_i = 0.170$, Table 2-6), which only differed in structure by the addition of the GrHgt variable. Twelve models were within the 90% confidence set (Table 2-6). Interestingly, 10 of those models contained the SBint variable and 11 contained the Gr variable. Coefficient estimates were similar across most top models and I chose to make inferences on the top AIC$_c$-selected model (#25). Deviance explained for nest occurrence models at this area scale (between 16-21% across top models) was less than at other scales (Table 2-6). Sage-grouse continued to select for greater shrub (sagebrush at this scale) cover, even at this 15-m radius area surrounding nest sites, as a positive increasing function, not a quadratic ($\beta_{SBint} = 0.398 \pm 0.128$, Table 2-7). Selection for greater grass cover also was evident, although weak ($\beta_{Gr} = 0.044 \pm 0.023$, Table 2-7). Again the strength of evidence for sagebrush cover estimated by the intercept method was strong ($\sum w_i = 0.84$), and evidence weights also suggest selection is linear (SBint $\sum w_i = 0.54$), with sage-grouse selecting for the greatest cover, compared to weak support for mid-range sagebrush cover at this area scale (quadratic; SBint + SBint^2 $\sum w_i = 0.30$; Table 2-8). The top AIC$_c$-selected nest occurrence model (#25) at the 15-m radius had good fit (LR $\chi^2_3 = 16.25$, $P < 0.001$), good accuracy ($ROC_{train} = 0.775$, $ROC_{test} = 0.761$), and prediction ($PCC_{train} = 71.0\%$, $PCC_{test} = 75.0\%$) was reasonable (Table 2-9).

Of the models with additional parameters, model #25-3 with SBstem was the top AIC$_c$ model and had good fit (LR $\chi^2_2 = 54.70$, $P < 0.0001$). There was weak support ($w_i = 0.351$) within my candidate set of additional parameter models and the deviance explained (18.51%) only improved marginally over the original model (15.82%, Table 2-12). Again, the SBint and Gr coefficients were robust after the addition of the additional SBstem variable (see Table 2-7) with strong selection still evident for greater sagebrush cover but weak selection for greater grass cover (Table 2-13). Selection for SBstem was moderate ($\beta_{SBstem} = 0.260 \pm 0.148$, Table 2-13), however, this model had good accuracy ($ROC_{train} = 0.779$) and reasonable prediction ($PCC_{train} = 72.43\%$, Table 2-14).

4.3. Proportional hazards survival analyses

Thirteen survival models were poorly specified using the Cox proportional hazards approach (χ^2 goodness-of-fit test of the nonzero slopes, $P < 0.05$) and these models were dropped as candidate models for both survival and occurrence modeling (see Table 2-2b). The same survival model (#22) was the top AIC$_c$-selected model at all three scales tested, and was different from the top occurrence model at each scale (Table 2-15 to 2-17). In general, the fit, accuracy, prediction, and variation that could be explained for nest survival models were lower than for occurrence models at all scales.

4.3.1. Survival at the nest site scale

The top AIC$_c$-selected nest site survival model (#22) had weak support (w_i = 0.349), but similar to the occurrence models at this scale, all 6 top models within the 90% confidence set contained the Bush + Bush^2 variables (Table 2-15). Inferences based on this model indicate that sage-grouse nests with mid-high range bush cover above the nest (β_{Bush}= 0.954 ± 0.019, β_{Bush2} = 1.000 ± 0.0003, convex function, Table 2-18) have a reduced risk of failure. The risk of failure was also reduced with increasing forb cover (β_{Forb} = 0.944 ± 0.030, moderate effect) and increasing grass height (β_{GrHgt} = 0.997 ± 0.007, weak effect, Table 2-18). Similar to the occurrence models at the nest site, the Bush + Bush^2 term had strong evidence of importance ($\sum$wi = 0.93), but Forb was also an important variable ($\sum w_i$ = 0.87, Table 2-19). Not surprisingly, all four models that contained these variables (models 22, 18, 20, and 24, Table 2-15) explained the greatest deviance (all ≈ 29% deviance explained). Finally, like the occurrence model at the nest site, variable importance weightings suggest limited importance of sagebrush in determining nest fate when not combined with other shrubs in the Bush + Bush^2 variable ($\sum w_i$ = 0.93; Table 2-19).

This nest site survival model (#22) had good fit (LR χ^2_4 = 19.50, P < 0.001), but only moderate-to-good model accuracy (ROC$_{train}$ = 0.717, ROC$_{test}$ = 0.727, Table 2-20).

Model prediction was lower for survival models (PCC_{train} = 71.4%, PCC_{test} = 68.4%; Table 2-20) compared to occurrence models at the nest-site scale. After classifying nests within my training dataset as failed (1) or successful/censored (0) by predicting the top model with the optimal cut-off point, I could easily differentiate nest survival to 28 days between the two groups (Successful = 55.17 ± 8.4%, Failed = 17.9 ± 5.7%; Log-rank χ^2_1 = 23.82, $P < 0.0001$). When this model was applied to my testing dataset, survival differed greatly between the two groups (Successful = 51.3 ± 10.9%, Failed = 15.4 ± 10.0%), but due to similar survival functions over the first half of incubation, the Log-rank test was weaker at detecting differences (χ^2_1 = 23.82, $P = 0.052$).

The additional-parameters model with Resid (model #22-2) was the top AIC_c-selected model. This model had good fit (LR χ^2_5 = 23.14, $P < 0.001$) but weak support ($w_i = 0.46$) within my candidate set of additional parameter models (Table 2-21). Resid only increased the deviance explained by 4% from the original model (Table 2-20). Accuracy and prediction were not improved by the addition of Resid to the original nest-site-survival model (ROC_{train} = 0.719, PCC_{train} = 69.2%; Table 2-20). Similar to the top model without Resid, however, this additional parameter model still predicted well on the training dataset, accurately differentiating survival for the censored nests (52.56 ± 8.48%) from those that failed (20.20 ± 5.92%; Log-rank χ^2_1 = 19.89, $P < 0.0001$). Surprisingly though, as Resid increased at the nest site, risk of nest failure also increased (β_{Resid} = 1.027 ± 0.014), although only moderately so (CI range 1.001-1.054; Table 2-18). Similarly, across most survival models tested containing the grass cover variable at the nest-site scale, there was a trend for increased risk of nest failure with increasing grass cover ($\beta_{grass} > 1.0$), but inferences were weak due to 95% CI that overlapped 1 for all models. Figure 2-2 graphically shows these relationships between nest failure and each parameter for model #22-2 at the nest site scale. Thresholds identified at the optimal cut-off point predict nest survival with Bush >20 % cover, GrHgt >50 cm tall, Forb >6 % cover, and Resid <2 % cover.

4.3.2. Survival at the 7.5-m patch scale

Twelve survival models at the patch scale were within the 90% confidence set (Table 2-16). The top AIC_c-selected model (again model #22) had weak support (w_i = 0.310), but explained slightly more deviance (32.75%; Table 2-16) than at the nest-site scale (29% Table 2-16). Inferences about parameters were similar to those at the nest site, but not as strong. The smaller Bush coefficient suggested a greater benefit with mid-to-high range bush cover than at the nest site scale, (smaller β_{Bush}), the effect was not as strong, with larger variance around those estimates ($\beta_{Bush} = 0.935 \pm 0.036$, $\beta_{Bush2} = 1.001 \pm 0.001$; convex function; Table 2-18). At this scale, however, greater forb cover ($\beta_{Forb} = 0.937 \pm 0.030$) and taller grass ($\beta_{GrHgt} = 0.980 \pm 0.001$) both strongly reduced the risk of nest failure; i.e., smaller coefficients with 95% CI that did not include 1 (Table 2-18).

There were no obvious trends in the parameters included within the top 12 models, but the variable importance weightings suggested that nest survival at the 7.5-m scale was more strongly influenced by herbaceous understory than shrub canopy. Both the GrHgt term ($\sum w_i = 0.95$) and the Forb term ($\sum w_i = 0.84$) had strong evidence of importance, whereas the Bush and sagebrush terms all had moderate to weak evidence of importance (all $\sum w_i \leq 0.60$; Table 2-19). This top 7.5-m, nest-survival model (#22) had good fit (LR $\chi^2_4 = 22.22$, $P < 0.001$), low-to-good model accuracy ($ROC_{train} = 0.750$, $ROC_{test} = 0.631$, Table 2-20), but poorer prediction ($PCC_{train} = 65.9\%$, $PCC_{test} = 55.3\%$, Table 2-20). However, when predicting survival with this top model on both my training (Survived = 52.0 ± 7.9%, Failed = 18.6 ± 6.3%) and testing datasets (Survived = 43.4 ± 9.1%, Failed = 0.0% - no nests hatched for this group), I could accurately differentiate failed from successful nests (Training: Log-rank $\chi^2_1 = 15.44$, $P < 0.0001$; Testing: Log-rank $\chi^2_1 = 4.94$, $P = 0.026$).

The addition of either Resid or Robel to nest-survival model #22 at the patch scale resulted in slightly improved deviance estimates, but the penalty for additional parameters resulted in the more parsimonious base model being selected (Table 2-22). Of the additional-parameter models, the base model had only moderate support (w_i = 0.516), primarily because model structure (parameters) changed little across candidate models. Further inspection of coefficients across each model revealed the 95% CI overlapped 1 for both Resid and Robel, suggesting limited importance of these parameters at driving nest fate at the 7.5-m scale. Thus, I assessed the relationship between nest failure and each parameter for model #22 at the 7.5-m patch scale (Figure 2-3). Optimal cut-off points suggest thresholds at which nest survival is predicted for Bush >5 % cover, GrHgt >17 cm tall, and Forb >3 % cover at the patch scale.

4.3.3. Survival at the 15-m area scale

Seven survival models at the 15-m area scale were within the 90% confidence set (Table 2-17). The top AIC$_c$-selected model was again model #22, which also had weak support (w_i = 0.432) but good deviance explained (34.6%, Table 2-17). Variable importance weights suggested the herbaceous understory (Forb $\sum w_i = 0.855$, Grass $\sum w_i =$ 0.874) as well as the shrub layer (Bush + Bush^2 $\sum w_i = 0.830$) were important in predicting nest survival at this large-area scale, with the importance of sagebrush enhanced when combined with all shrubs (i.e., Bush terms; Table 2-19). Inferences about this model were similar to other scales (LR $\chi^2_4 = 22.22$, $P < 0.001$), with risk of failure reduced with moderate-to-high bush cover ($\beta_{Bush} = 0.918 \pm 0.044$, $\beta_{Bush2} = 1.000 \pm 0.002$), greater forb cover ($\beta_{Forb} = 0.956 \pm 0.025$), and taller grass ($\beta_{GrHgt} = 0.979 \pm 0.011$, Table 2-18). However, all effects were weak (95% CI just overlap 1; Table 2-18). With only good-to-poor model accuracy ($ROC_{train} = 0.766$, $ROC_{test} = 0.531$) and poor prediction ($PCC_{train} = 69.3\%$, $PCC_{test} = 55.3\%$) my models were weakest at capturing mechanisms of nest failure at the 15-m scale. I could predict survival accurately using this top model and cut-point for my training dataset (Survived = 52.3 ± 8.2%, Failed = 17.0 ± 6.0%; Log-rank $\chi^2_1 = 14.47$, $P = 0.0001$), but I had poor predictive ability when applied to the testing dataset (Survived = 40.7 ± 11.8%, Failed = 37.0 ± 11.9%; Log-rank $\chi^2_1 = 0.29$, $P = 0.587$).

Additional parameters Resid and Robel resulted in minor improvements in deviance explained (Table 2-23), but similar to the patch scale, the base model #22 was selected as the top AIC_c model again, with only weak support ($w_i = 0.342$; Table 2-23). All models containing the additional parameters Resid and Robel added little power to explain nest survival at the 15 m area scale (95 % CI overlapped 1 in all cases). Thus, similar to the patch scale, I used model #22 to graphically show the relationship between nest failure and each parameter at the 15 m nest area scale. Optimal cut-off points suggest thresholds at which nest survival is predicted for Bush >7 % cover, GrHgt >27 cm tall, and Forb >7 % cover at the 15 m area scale.

5. Discussion

My models were excellent at predicting sage-grouse nest selection (occurrence) in southern Alberta. Even when predicted on an independent sample of data, the models validated well, with high prediction and classification accuracy (Table 2-9). With the additional parameters in the top models, I could explain as much as 73% of the variation in nest occurrence (Table 2-14). The best predictions were at the nest-site scale. Hierarchical habitat selection by sage-grouse for nest sites is evident, with different parameters selected at different scales; the area, the patch, and the nest-site scales. As expected, sage-grouse selected for nest habitats that provide structural cover from shrubs (sagebrush and other shrubs) as well as from herbaceous understory vegetation that concealed the nest. Selection is strong for a large area (15-m radius scale) of thick sagebrush cover which contains greater amounts of grass (moderate selection, Table 7). Within this area, females again selected strongly for a patch (7.5-m radius scale) of dense sagebrush (quadratic function), although the densest patches are avoided. Patches containing taller grass (Table 2-7) and greater visual obstruction cover were selected (Table 2-13). Finally, within this patch, females chose to place their nest under sagebrush, but appear to shift their focus to include cover provided by additional shrubs immediately surrounding the nest site (Tables 2-7, 2-13), again avoiding the densest canopies. Wiebe and Martin (1998) found that white-tailed ptarmigan (*Lagopus leucurus*) also selected for intermediate cover at the nest site. They suggest that females are making a trade-off that allows for a better view of predators within the nest surrounding (Wiebe and Martin 1998). Sage-grouse also may be recognizing these ecological cues similarly, selecting for intermediate-to-high shrub cover, because nest failure was reduced for those selecting moderate ranges of cover.

Within the patch scale, taller grass cover still is selected strongly at the nest site (Table 2-7), along with enhanced visual obstruction cover and additional nest concealment provided by woody sagebrush stem (Table 2-13). Habitat with high obstruction or concealment cover has been shown to be important for nesting for several other grouse species (Lutz et al. 1994; Wiebe and Martin 1998; Manzer 2004) as well as sage-grouse (Gregg et al. 1994), and survival can be enhanced with increased concealment cover (Lutz et al. 1994; Manzer 2004).

Variable importance weightings are useful for making generalizations about the relative importance of variables within a candidate set of models. Weights for variables from occurrence models also suggest that hierarchical selection is taking place. For example, weights highlight the importance of dense sagebrush cover in the area surrounding a nest, and the importance of moderate cover of sagebrush patches within that area. The overwhelming importance of moderate-to-high range cover of additional shrubs at the nest site was also evident from the variable importance weights (Table 2-8). Grass height was an important variable at all scales tested, increasing in importance closer to the nest site (Table 2-8). Together, these importance weights reinforce the significance of both shrub-canopy cover and herbaceous-obstruction cover selected by female sage-grouse for nesting. A tall shrub canopy is necessary to conceal nests from avian predators, and tall herbaceous understory also is necessary, possibly acting as a visual barrier obscuring nests (Martin 1993; Crawford et al. 2004) from terrestrial predators.

When using variable importance weights, Burnham and Anderson (2002: 169) suggest ensuring "a balance in the number of models that contain each variable" so as to "put each variable on equal footing." Although I had high variability in the number of candidate models for which each variable occurred, I chose to identify biologically meaningful models *a priori,* rather than 'cook' my candidate set to have even variable occurrence across all models. This may influence the relative variable importance, but in many cases, I saw variables that occurred in few models, such as the Bush + Bush^2 variable (in 6 of 23 occurrence models at the nest site scale) have the greatest variable importance ($\sum w_i \geq 0.99$, Table 2-8), and variables such as Forb that were in over twice as many models (in 13 of 23 occurrence models at the area scale), have relatively low variable importance ($\sum w_i \geq 0.27$; Table 2-8). Thus, I feel that the importance weights are valid relative measures of the strength of variable importance in my models, and also add support to my decision to make inferences using the top AIC$_c$-selected model within each candidate set.

Hierarchical selection of habitat by wildlife species is not a new concept (Meyer et al. 1998; Breininger et al. 1998; Johnson et al. 2001; Boyce et al. 2003; Mcgrath et al. 2003), although often only a single scale of selection is addressed. Although Aldridge and Brigham (2002) have addressed hierarchical selection by sage-grouse with selection at multiple scales for sagebrush, my models incorporating more complex designs illustrate detailed and differing selection patterns across these hierarchical scales. My results suggest that nesting habitat requirements are not uniform surrounding a nest site, nor across a landscape. Management focused on nest site characteristics alone, which has been the focus of many nesting habitat studies for prairie grouse (Gregg et al. 1994; Lutz et al. 1994; Sveum et al. 1998b), could lead to sub-optimal habitat provisioning for the species of interest.

Sage-grouse nest success varies widely across the species range (15-86%) but is typically between 30-60% (see Schroeder et al. 1999). Nest survival in my study (35.3 ± 5.37%) was at the low end of this range, and slightly lower than previous research in Alberta from 1998-1999 (46%, n = 29, Aldridge and Brigham 2001). However, as Aldridge and Brigham (2001) suggest, above normal spring precipitation, which has been positively correlated with nest success (Gill 1966), may result in elevated nest success. My study spanned the final 2 years (2000-2001) of an extreme 3-year drought period in southern Alberta, possibly resulting in slightly lower nest success. However, I did not detect differences in nest success between grouped years for my training (2001-2003) and testing (1998-2000) datasets (Log-rank $\chi^2_1 = 0.27$, $P = 0.61$).

Given that females are highly selective, it is not surprising that the predictive capabilities for my nest survival models were lower, particularly for the independent (1998-2000) nest validation sample. I believe that this may also be a sample size issue, having only 40 nests with 22 failures in my validation dataset. Survival analyses with <25 samples per treatment group rarely provide adequate results, and in most cases, 50 samples per group are required (Pollock et al. 1989; Winterstein et al. 2001). As is the case for most wildlife telemetry studies, particularly when data are limited for endangered species, one can not often afford to partition samples into model training and testing datasets. Even though nest success was greater in prior years (testing dataset) and my testing dataset sample size was small, I was still able to differentiate failed from successful nests at most scales.

Occurrence models indicated females select for mid-high shrub cover (Bush variable) at the nest site only. However, survival models at all scales (model #22) suggest that females who select for shrub cover at the nest site as well as the larger patch and area scales surrounding the nest are more likely to be successful. The Bush parameter was largely composed of sagebrush, with other shrubs adding between 2-6% additional canopy cover (Table 2-1). Thus, selection for only sagebrush may result in similar nest success. This was not the case however, and importance weights over all survival models indicate that the Bush + Bush^2 played a greater role in nest survival than sagebrush alone, or using the combined weights for all sagebrush variables (Table 2-19). Other research has shown that sage-grouse tend to select more dense sagebrush to place their nests under, and nests with greater canopy cover are more successful (Klebenow 1969; Wallestad and Pyrah 1974; Connelly et al. 1991; Gregg et al. 1994; Sveum et al. 1998b; Aldridge and Brigham 2002). However, in Alberta, cover from sagebrush is limited (5-10%, my study and Aldridge and Brigham 2002) compared to that in other areas (Schroeder et al. 1999; Connelly et al. 2004). Thus, females may recognize the general importance of canopy structure and select for additional cover provided by other shrubs, at least at the nest site itself. Beyond the nest site, additional shrub cover also reduces the risk of failure, but females are not as efficient at recognizing cues at these scales as shrubs were not selected for in the occurrence models, possibly creating ecological traps (Delibes et al. 2001; Donovan and Thompson 2001). Bock and Jones (2004) found a negative relationship between population density and reproductive success for many bird species when present in human-disturbed habitats. They suggested that birds fail to recognize these ecological traps when the human-altered landscape differed from that in which the birds evolved. Sage-grouse appeared to focus on sagebrush as the most important component of nesting habitat, but reductions in sagebrush availability, possibly from human-related causes (discussed below), may have increased the importance of other shrubs; a benefit sage-grouse fail to recognize beyond the nest site itself.

Residual grass was correlated with total grass cover, preventing the addition of Resid to the additional parameters occurrence models. However, females did not show selection or avoidance of residual grass cover at any scale in univariate models (see Table 2-1 for means). Although I expected residual grass cover to be greater at successful nests, this was not the case. Survival at the nest-site scale (i.e., within 0.5 m of the nest) was reduced with increasing residual grass cover (Successful = 9.2 ± 1.6%; Failed = 4.9 ± 1.0%; Figure 2-3). This relationship did not exist at other scales; at the patch and area scales, 95% CI for β_{Resid} for model #22-2 overlapped 1. McKee et al. (1998) found that excessive litter (>25%), defined as horizontally oriented vegetation from the previous year, resulted in reduced nest success for greater prairie-chickens (*Tympanuchus cupido pinnatus*) in Missouri. Although I do not believe that there was an excessive build up of residual plant material during my study (8% residual grass cover, Table 2-3), it has been suggested that new plant growth, and thus height of nest cover vegetation, may be delayed by a build up of matted dead matter (Westemeier 1973; Mckee et al. 1998). However, this is not likely to occur in the xeric dry mixedgrass ecosystem of southern Alberta. Although grass height and residual grass cover were not correlated ($r_s \leq 0.16$, n = 186, for all three scales), it is possible that reduced residual-grass cover at successful nest sites is a result of selection for taller herbaceous vegetation, which reduces the risk of nest failure.

Despite exhibiting strong selection of tall grass for nest concealment at all scales, grass height was still an important contributor to nest survival at all scales. Conversely, although females did not select for forbs at any scale, nest success increased for those that selected greater forb cover; a trend detected across all scales. This reinforces the importance of surrounding tall herbaceous understory vegetation or lateral cover for successful nesting (Wallestad and Pyrah 1974; Gregg et al. 1994; Sveum et al. 1998b; Aldridge and Brigham 2002; Watters et al. 2002), and may reflect larger patch-level ecological cues that are not being recognized by sage-grouse. In addition, given that forbs could enhance nest success, and the diet for precocial sage-grouse chicks immediately after they hatch (Johnson and Boyce 1990; Sveum et al. 1998a; Aldridge and Brigham 2002), it is surprising that females do not recognize these benefits and choose to nest in areas with greater forb cover.

Variable importance weights suggested forbs (palatable to sage-grouse) contributed strongly to survival models at all three scales (Table 2-19). Grass height had strong evidence of support at the patch and area scales, and moderate importance at the nest site, again supporting the importance of herbaceous understory vegetation (Wallestad and Pyrah 1974; Gregg et al. 1994; Sveum et al. 1998b; Aldridge and Brigham 2002; Watters et al. 2002). There was strong variable importance for the Bush + Bush^2 parameter (moderate-high cover) at both the nest site and the 15-m area scale, but only moderate importance at the 7.5-m patch scale. There was additional evidence in support of the importance of sagebrush (SBint parameter) for the patch-scale survival models, although it was weak (Table 2-19).

Based on the variable importance weights for both occurrence and survival models, the line intercept technique (Canfield 1941) is a better approach for measuring sagebrush canopy cover (to correlate with sage-grouse nest site selection and nest success) than using 1-m^2 quadrats. Although these two methods are correlated, and as Daubenmire (1959) pointed out, too few quadrats may result in highly variable and possibly overestimated canopy measures for shrubs. Both measures produced similar mean cover estimates (Table 2-1) in my study, but future research conducted on sagebrush-steppe habitats should use the line intercept method to assess sagebrush (and shrub) canopy coverage, as recommended by the sage-grouse management (Connelly et al. 2000) and monitoring (Connelly et al. 2003) guidelines.

Even though most nests (81%) were at least partially located under sagebrush, many were covered or surrounded by other shrubs such as snowberry (*Symphoricarpos albus*), rose (*Rosa* spp.), greasewood (*Sarcobatus vermiculatus*), wolf willow (*Elaeagnus commutata*), and occasionally creeping juniper (*Juniperus horizontalis*). Not surprisingly then, nest fate was directly affected by other shrubs (Bush + Bush^2 parameters), and this relationship existed at all three scales measured (nest site, 7.5-m patch scale, and 15-m area scale). Thus, sage-grouse are only partially recognizing ecological cues linked to fitness. Other studies have shown that nest survival is unrelated to the shrub species the nest is placed under (Sveum et al. 1998b; Aldridge and Brigham 2003) while others still have shown that success is reduced when nests are not placed under sagebrush (Connelly et al. 1991). I show that nest success could actually be enhanced when shrubs, in addition to sagebrush, are selected. Given that sagebrush is not abundant within the Alberta range of sage-grouse (~2% cover at random areas and 12-14% cover at the random sites; Table 2-1) compared other areas throughout the range (15-25%; Schroeder et al 1999; Connelly et al. 2000), sage-grouse may be selecting for additional cover from other shrubs. As Aldridge and Brigham (2003) pointed out, as long as suitable shrub cover is available, the species providing it might not matter.

My predictive models allow me to make inferences and identify threshold levels for parameters in my models. Given that the same survival model (#22) with the same parameters was selected at all three scales, pasture-level management providing vegetation that meets or exceeds these model thresholds will increase nest success for sage-grouse. Although trends were similar at all scales, I discuss in detail here predictions and thresholds based on the 7.5-m radius scale for three reasons. Firstly, management of shrubs and herbaceous understory does not take place at the scale of a single sagebrush plant and the vegetation within a 1-m^2 quadrat surrounding it. Management takes place at the scale of a large habitat patch, or pasture, thus, I felt that the patch or area scale (7.5 m or 15 m) would be more appropriate. Secondly, my models indicate that selection is taking place beyond the nest site itself, and that nest fate can be affected by vegetation at these greater patch and area scales. Finally, my survival model at the patch scale was more accurate and had better predictive capacity than the 15-m area scale model. Given that the relationship between nest survival and each parameter is similar for all scales, when managing habitat for conservation purposes, I recommend the more conservative (i.e. greater cover or height threshold) be used. Several management options may exist that could achieve these desired goals (i.e., various grazing strategies, active management of sagebrush, etc.), but I recommend these approaches be tested within the experimental framework of an adaptive management process (Chapter 5, Aldridge et al. 2004).

Small increases in sagebrush cover on the landscape (i.e., 5-10%) might be enough to elevate productivity to stabilize productivity in the Alberta sage-grouse population (Aldridge and Brigham 2002). Using β_i coefficients, presented here as exponentiated estimates or risk of nest failure for a single unit increase in a particular parameter, I can assess the risk of failure for varying availabilities of the parameter of interest. For the patch survival model (#22), the combined estimates for β_{Bush} and β_{Bush2} (Table 2-18) indicates the risk of nest failure ($\beta_{Bush} + \beta_{Bush2} = 0.9353$) decreases by about 7% for each 1% increase in bush cover; although this relationship is not linear. Thus, if bush cover was increased by 5%, nest failure ($\beta_{Bush} + \beta_{Bush2} = 0.7248$) would be reduced by about 27%. A 10% increase ($\beta_{Bush} + \beta_{Bush2} = 0.5398$) will cut nest failure rates by about half. An increase of sagebrush cover (the primary component of Bush) by 5-10%, would provide enhanced breeding habitat for sage-grouse, providing 15-20% cover in Alberta, and double the chance of nests successfully hatching. This can be seen graphically in Figure 2-3a, where I assess the relative nest failure hazard by varying the bush parameter while keeping all other parameters at their mean values. An increase in bush cover from that currently available (~5%, Table 2-1) to >10%, would result in the majority of habitat falling below the optimal cut-point, and drastically reduce the risk of nest failure (Figure 2-3a). Similarly, at >15% bush cover, there is little change in the risk of nest failure, suggesting a potential management target where the greatest increase in nest success per unit increase in sagebrush will be achieved. These thresholds strongly support suggested the minimum management target of 15% sagebrush cover for sage-grouse breeding habitat (Connelly et al. 2000).

Although sagebrush stem was selected at both the nest site and the 15-m area scales, I was unable to test the effect of stem on nest survival due to the SBstem parameter violating the proportional hazards assumption. I hypothesize however, that selection for sagebrush stem, and the Bush parameter (combined sagebrush + other shrubs) is likely a consequence of females recognizing the importance of structural cover, and selecting for it regardless of the type. This also might suggest a lack of suitable sagebrush cover on the landscape. *A. cana* is one of the few fire-successional *Artemisia* species that resprouts vegetatively after spring fires (Tisdale and Hironaka 1981; Wambolt et al. 1990; Adams et al. 2004). Reduced fire frequencies associated with fire suppression on the Canadian prairies (Adams et al. 2004) may result in decreased sagebrush abundance, rendering plants older and more decadent. Recent drought conditions have reduced the number of episodic flood events, which can also enhance the resprouting of *A. cana*. (Adams et al. 2004). Combined, the reduced abundance of vigorous and mature, but not decadent sagebrush, could potentially limit high-quality habitats required to maintain viable populations of sage-grouse, as well as other sagebrush obligates on the dry mixedgrass prairie. This relationship needs to be explored further.

Ideally, to truly represent habitat quality through assessing fitness, one must include measures of both survival and reproduction. Here, I have used one measure of reproduction (nest survival) as a surrogate for fitness. As Franklin et al. (2000) illustrate for spotted owls, habitat variation can affect components of fitness very differently.

Thus, while my nest models may not capture fully all processes linked to fitness (i.e., brood survival and habitat use, and female survival and habitat use across different seasons), and I did not directly assess any measures associated with human use, I feel that these models are an important initial step that provide managers with the tools necessary to provide high-quality nesting habitats for sage-grouse in Alberta, and ensure females are likely to use those habitat and be successful in doing so.

6. Conclusions

Based on my nest occurrence and survival models, management for sage-grouse nesting habitats in southern Alberta should be aimed at providing 1) suitable abundance of healthy sagebrush cover, and 2) suitable cover and height of herbaceous understory vegetation. Given the low availability of sagebrush in Alberta, females are selecting for sagebrush (patch and area scales) and additional shrub cover (nest site scale) at nests. Nest success is driven strongly by shrub cover and could be improved with slight increases in sagebrush abundance. The ecology of silver sagebrush is poorly understood (Adams et al. 2004), and potential management actions following an adaptive management approach (Aldridge et al. 2004) would be beneficial to increase knowledge and means to improve range health in sagebrush habitats. In doing so, one must continue to monitor how sage-grouse respond to management actions. Initial management goals should be aimed at maintaining or enhancing sagebrush, resulting in large areas with overall cover of 10-20% (Figures 2-3, 2-4). Within these areas, heterogeneous patches should exist, some with 30 to 40% cover, which will increase the chance of birds using these habitats and also enhance nest success.

The importance of herbaceous understory vegetation in providing high-quality sage-grouse nesting habitat has been recognized by others (Gregg et al. 1994; Sveum et al. 1998b; Connelly et al. 2004; Crawford et al. 2004). I provide models identifying understory vegetation thresholds at multiple scales that must be maintained if areas are to be selected, and successfully used for nesting by females, ensuring productive populations. Thresholds suggest that managers should strive to maintain grass within sagebrush habitats that is 18-30 cm in height with a healthy forb component of at least 6% forb cover; greater cover of forbs (10-15%) will increase the likelihood of nest survival. Within those areas, ensuring some patches have sites with even taller grass (>50 cm) to provide additional structural cover necessary to conceal nests will further reduce the risk of nest failure. My results suggest that mid-seral range conditions may be of greater value than more traditional manament for late-seal or more climax communities.

Even though inferences from prior research identify cursory nesting habitat requirements for sage-grouse in Alberta, and go so far as to suggest that sagebrush may be limiting (Aldridge and Brigham 2002), management efforts have yet to result in any on-the-ground initiatives to enhance habitat for this endangered population. While numbers continue to decline, managing for high quality habitat to ensure productive populations is increasingly important, especially given the devastating consequences that stochastic events such as West Nile virus pose (Naugle et al. 2004). My threshold models provide managers with the tools necessary to begin implementing practices to enhance sage-grouse habitats in Alberta. I hope that these tools will be used to identify and maintain critical (nesting) habitat for sage-grouse, as required by the Federal Species at Risk Act (SARA).

Table 2-1. Explanatory variables, means and standard errors (in parentheses) of values used to assess nest fate and occurrence for 93 nest sites and 93 paired random nest locations at three scales in southeastern Alberta from 2001-2003. When grass was absent, height values were considered zero.

Variable		Site (center quadrat)		7.5-m patch radius		15-m area radius	
code	Description	Nest	Random	Nest	Random	Nest	Random
SBint	Sagebrush cover (%) estimated using line intercept	25.46 (1.92)	14.89 (1.12)	4.17 (0.38)	1.95 (0.20)	2.24 (0.28)	1.10 (0.15)
SB	Sagebrush cover (%) estimated with a 1m^2 quadrat	23.82 (1.95)	12.42 (1.02)	4.25 (0.52)	2.08 (0.26)	3.13 (0.37)	1.94 (0.29)
Bush	% cover of all shrub (including sagebrush) estimated with a 1m^2 quadrat	30.70 (2.10)	14.68 (1.13)	9.09 (0.97)	4.74 (0.71)	7.36 (0.92)	4.17 (0.56)
Gr	Grass cover (%) estimated with 1m^2 quadrat	19.56 (1.72)	18.87 (1.55)	21.35 (1.37)	18.75 (1.41)	21.92 (1.48)	19.35 (1.34)
GrHgt	Mean maximum Gr Hgt (cm) within each 1m^2 quadrat	33.94 (2.10)	27.40 (1.80)	27.90 (1.45)	23.76 (1.45)	26.94 (1.36)	23.52 (1.39)
Forb	Forb cover (%) estimated with 1m^2 quadrat	3.82 (0.55)	5.59 (0.68)	6.05 (0.62)	6.77 (0.82)	6.44 (0.69)	6.72 (0.87)
ForbOth	Unpalatable (to sage-grouse) forb cover (%) estimated with a 1m^2 quadrat	0.38 (0.14)	0.70 (0.21)	0.51 (0.11)	0.86 (0.16)	0.71 (0.12)	0.91 (0.17)

Table 2-2. Shrub and herbaceous component models used to generate *a prior* candidate models are shown in (a) for nest site occurrence modeling and survival based on 93 nest sites and 93 paired random nest locations in southeastern Alberta from 2001-2003. Each of the six shrub component models were combined with each of the six herbaceous component models, for a total of 36 different initial candidate models (b). Thirteen models marked asterisk (*) were removed due to violations of the proportional hazards assumption for survival models, leaving 23 candidate models for survival and occurrence modeling.

a)

Shrub Component Variables	Herbaceous Component Variables
SB	Gr
SB + SB^2	Gr + GrHgt
Bush	Gr + Forb
Bush + $Bush^2$	Gr + GrHgt + Forb
SBint	Forb + GrHgt
SBint + $SBint^2$	Gr + GrHgt + Forb + ForbOth

b)

#	Structure for Sagebrush Quadrat Models	#	Structure for Bush Models	#	Structure for Sagebrush Intercept Models
1-	SB + Gr	*13-	Bush + Gr	25-	SBint + Gr
2-	SB + SB^2 + Gr	14-	Bush + $Bush^2$ + Gr	26-	SBint + $SBint^2$ + Gr
3-	SB + Gr + GrHgt	*15-	Bush + Gr + GrHgt	27-	SBint + Gr + GrHgt
4-	SB + SB^2 + Gr + GrHgt	16-	Bush + $Bush^2$ + Gr + GrHgt	28-	SBint + $SBint^2$ + Gr + GrHgt
*5-	SB + Gr + Forb	*17-	Bush + Gr + Forb	*29-	SBint + Gr + Forb
*6-	SB + SB^2 + Gr + Forb	18-	Bush + $Bush^2$ + Gr + Forb	*30-	SBint + $SBint^2$ + Gr + Forb
7-	SB + Gr + GrHgt + Forb	*19-	Bush + Gr + GrHgt + Forb	31-	SBint + Gr + GrHgt + Forb
8-	SB + SB^2 + Gr + GrHgt + Forb	20-	Bush + $Bush^2$ + Gr + GrHgt + Forb	32-	SBint + $SBint^2$ + Gr + GrHgt + Forb
*9-	SB + Forb + GrHgt	*21-	Bush + Forb + GrHgt	33-	SBint + Forb + GrHgt
*10-	SB + SB^2 + Forb + GrHgt	22-	Bush + $Bush^2$ + Forb + GrHgt	34-	SBint + $SBint^2$ + Forb + GrHgt
11-	SB + Gr + GrHgt + Forb + ForbOth	*23-	Bush + Gr + GrHgt + Forb + ForbOth	35-	SBint + Gr + GrHgt + Forb + ForbOth
*12-	SB + SB^2 + Gr + GrHgt + Forb + ForbOth	24-	Bush + $Bush^2$ + Gr + GrHgt + Forb + ForbOth	36-	SBint + $SBint^2$ + Gr + GrHgt + Forb + ForbOth

Table 2-3. The additional explanatory parameters, means, standard errors (in parentheses) and range of values used to assess nest occurrence for 92 nest sites and 92 paired random nest locations at all three scales in southeastern Alberta from 2001-2003 are shown in a). Observations were not recorded for one nest pair which was dropped. The model structure of additional parameters added to the top AIC$_c$-selected model at each scale is shown in b). Note: All models with SBstem violated the proportional hazards assumption, and thus those models were dropped only as candidate survival models. Residual grass (Resid) was highly correlated with grass cover ($r > 0.70$) and was not used in candidate models where the top 2001-2003 AIC$_c$-selected model at that scale contained Gr (this was the case for all occurrence models only).

a)

Variable code	Description	Site (center quadrat)		7.5-m patch radius		15-m area radius	
		Nest	Random	Nest	Random	Nest	Random
Robel	Visual obstruction reading (height in cm) measured at 2m from pole	26.33 (1.37)	13.14 (0.84)	8.43 (0.80)	5.43 (0.55)	6.53 (0.56)	5.08 (0.45)
SBstem	Cover (%) provided from sagebrush stem using a 1m^2 quadrat	14.40 (1.41)	5.63 (0.77)	2.09 (0.35)	0.86 (0.21)	1.02 (0.15)	0.58 (0.12)
Resid	Residual grass cover (%) estimated using a 1m^2 quadrat	7.76 (1.11)	8.37 (1.12)	8.61 (0.93)	8.01 (0.96)	8.93 (1.02)	8.06 (0.90)

b)

Model #	Structure for 2001-2003 additional parameters models
Top #	(Top AIC$_c$-selected model for any given scale)
Top #-1	(Top model) + Robel
Top #-2	(Top model) + Resid
Top #-3	(Top model) + SBstem
Top #-4	(Top model) + Robel + Resid
Top #-5	(Top model) + Robel + SBstem
Top #-6	(Top model) + Resid + SBstem
Top #-7	(Top model) + Robel + Resid + SBstem

Table 2-4. AIC_c-selected nest occurrence models, Akaike weights (w_i) for all models comprising a cumulative AIC_c weight ($\sum w_i$) of ≥ 0.90 at the nest site (center quadrat). All model Likelihood Ratio (LR) χ^2 tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	$\sum w_i$	Model LR χ^2	% Dev. Explained
16	Bush + $Bush^2$ + Gr + GrHgt	– 32.313	4	73.081	0.000	0.426	0.426	64.30	49.87
22	Bush + $Bush^2$ + Forb + GrHgt	– 32.589	4	73.633	0.552	0.324	0.750	63.75	49.44
20	Bush + $Bush^2$ + Gr + GrHgt + Forb	– 32.303	5	75.295	2.215	0.141	0.891	64.32	49.89
14	Bush + $Bush^2$ + Gr	– 35.599	3	77.467	4.387	0.048	0.938	57.73	44.78

Table 2-5. AIC$_c$-selected nest occurrence models, Akaike weights (w_i) for all models comprising a cumulative AIC$_c$ weight ($\sum w_i$) of ≥ 0.90 for the 7.5-m radius scale from the nest site. All model Likelihood Ratio (LR) χ^2 tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC$_c$	Δ_i AIC$_c$	w_i	$\sum w_i$	Model LR χ^2	% Dev. Explained
36	SBint + SBint^2 + Gr + GrHght + Forb + ForbOth	– 40.334	6	93.645	0.000	0.181	0.181	48.26	37.43
28	SBint + SBint^2 + Gr + GrHgt	– 42.713	4	93.880	0.236	0.160	0.341	43.50	33.74
34	SBint + SBint^2 + Forb + GrHgt	– 42.725	4	93.905	0.261	0.159	0.500	43.47	33.72
27	SBint + Gr + GrHgt	– 44.328	3	94.925	1.280	0.095	0.595	40.27	31.24
33	SBint + Forb + GrHgt	– 44.328	3	94.926	1.281	0.095	0.690	40.27	31.23
26	SBint + SBint^2 + Gr	– 44.429	3	95.128	1.484	0.086	0.776	40.07	31.08
35	SBint + Gr + GrHgt + Forb + ForbOth	– 42.224	5	95.138	1.494	0.086	0.861	44.48	34.50
32	SBint + SBint^2 + Gr + GrHgt + Forb	– 42.707	5	96.104	2.460	0.053	0.914	43.51	33.75

Table 2-6. AICc-selected nest occurrence models, Akaike weights (wi) for all models comprising a cumulative summed AICc weight ($\sum$wi) of $\geq$ 0.90 for the 15-m radius scale from the nest site. All model Likelihood Ratio (LR) $\chi 2$ tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	$\Delta_i\ AIC_c$	w_i	$\sum w_i$	Model LR χ^2	% Dev. Explained
25	SBint + Gr	53.986	2	112.105	0.000	0.173	0.173	20.95	16.25
27	SBint + Gr + GrHgt	52.934	3	112.138	0.033	0.170	0.342	23.06	17.88
26	SBint + $SBint^2$ + Gr	53.511	3	113.292	1.187	0.095	0.438	21.90	16.99
28	SBint + $SBint^2$ + Gr + GrHgt	52.472	4	113.398	1.293	0.090	0.528	23.98	18.60
33	SBint + Forb + GrHgt	53.599	3	113.469	1.364	0.087	0.615	21.73	16.85
31	SBint + Gr + GrHgt + Forb	52.889	4	114.232	2.128	0.060	0.675	23.15	17.95
14	Bush + $Bush^2$ + Gr	53.986	3	114.242	2.137	0.059	0.734	20.95	16.25
35	SBint + Gr + GrHgt + Forb + ForbOth	51.953	5	114.596	2.491	0.050	0.784	25.02	19.41
34	SBint + $SBint^2$ + Forb + GrHgt	53.092	4	114.638	2.533	0.049	0.832	22.74	17.64
36	SBint + $SBint^2$ + Gr + GrHgt + Forb + ForbOth	51.211	6	115.400	3.295	0.033	0.866	26.50	20.56
32	SBint + $SBint^2$ + Gr + GrHght + Forb	52.381	5	115.452	3.347	0.032	0.898	24.16	18.74
16	Bush + $Bush^2$ + Gr + GrHgt	53.702	4	115.858	3.753	0.026	0.924	21.52	16.69

Table 2-7. Estimated coefficients (β_i), standard errors (shown in parentheses), and 95% confidence intervals for top AIC$_c$-selected candidate nest occurrence models in south-eastern Alberta for all scales. Models were developed on 93 nest sites and 93 paired random locations collected from 2001-2003.

Variable	Nest Site Model 16	Confidence intervals		7.5-m radius Model 36	Confidence intervals		15-m radius Model 25	Confidence intervals	
		Lower	Upper		Lower	Upper		Lower	Upper
Bush	0.156 (0.056)	0.046	0.266						
[a]Bush^2	−0.069 (0.089)	−0.243	0.106						
SBint				0.792 (0.204)	0.392	1.192	0.398 (0.128)	0.147	0.649
[a]SBint^2				−2.807 (1.068)	−4.900	−0.714			
[a]Gr	1.573 (2.121)	−2.584	5.731	−2.074 (2.686)	−7.339	3.192	4.044 (2.348)	−0.558	8.645
[a]GrHgt	4.805 (2.063)	0.761	8.848	7.779 (3.716)	0.497	15.062			
[a]Forb				−1.766 (5.589)	−12.72	9.189			
ForbOth				−0.350 (0.172)	−0.687	−0.014			

[a]Coefficients, standard errors, and confidence intervals for Bush^2, SBint^2, Gr, GrHgt and Forb have been multiplied by 100.

Table 2-8. Relative variable importance for nest occurrence models (2001-2003), based on the sum of the AIC_c weights for each variable across all models. (n=93 nest sites and 93 paired random locations). Sagebrush variables below the double line illustrate the strength of the measurement technique (quadrats vs. line intercept) and the importance of the quadratic relationship at each scale. Parameter Model Freq. indicates the frequency for each parameter occurring across all 23 models.

	Parameter Model Frequency	Nest Site	7.5-m radius	15-m radius
Bush + $Bush^2$	6	0.9999	0.0027	0.1206
SB	4	0.0000	0.0001	0.0305
SB + SB^2	3	0.0000	0.0000	0.0102
Sbint	5	0.0000	0.3588	0.5388
SBnt + $SBint^2$	5	0.0000	0.6383	0.2999
Grass	20	0.6765	0.6505	0.6920
GrHgt	17	0.9363	0.8621	0.6354
Forb	13	0.5259	0.5110	0.2658
ForbOther	4	0.0453	0.2665	0.0882
All sagebrush (quadrats only)	7	0.0001	0.0002	0.0407
All sagebrush (intercept only)	10	0.0000	0.9971	0.8387
All sagebrush (linear)	9	0.0000	0.3589	0.5692
All sagebrush (quadratic)	8	0.0000	0.6383	0.3102
Any with sagebrush (both measurements)	17	0.0001	0.9973	0.8794

Table 2-9. Comparison of top AIC_c-selected nest occurrence models, metrics for overall model significance, fit, and classification accuracy for both training (93 nests from 2001-2003) and testing data (40 nests from 1998-2000) across different scales. All model Likelihood Ratio (LR) χ^2 tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model. The area under the receiver operating characteristic curves [ROC (SE)] and the percent correctly classified (PCC) based on the training dataset optimal cut off point were used to assess model classification accuracy.

Scale	Model	AIC_c-selected model		Model	% Dev.	Optimal	Training data		Testing data	
	#		AIC_c	LR χ^2	Explained	cut-off	ROC	PCC	ROC	PCC
Nest site	16	Bush + Bush^2 + Gr + GrHgt	72.847	64.30	49.87	0.5087	0.929 (0.020)	85.00	0.930 (0.028)	85.00
7.5-m radius	36	SBint + SBint^2 + Gr + GrHght + Forb + ForbOth	93.137	48.26	37.43	0.5005	0.873 (0.025)	78.49	0.884 (0.036)	82.50
15-m radius	25	SBint + Gr	111.971	20.95	16.25	0.5033	0.775 (0.035)	70.97	0.761 (0.056)	75.00

Table 2-10. Nest occurrence models and Akaike weights (wi) for additional parameter models at the nest site (center quadrat) for 92 nests and 92 paired random locations based on the initial 2001-2003 AIC_c-selected top model (#16). Combinations of additional parameters only measured in 2001-2003 for Robel pole, sagebrush stem cover, and residual grass cover comprised candidate models. All model Likelihood Ratio (LR) χ^2 tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model LR χ^2	% Dev. Explained
16-5	Bush + $Bush^2$ + Gr + GrHgt + Robel + SBstem	– 17.386	6	47.759	0.000	0.896	92.77	72.74
16-3	Bush + $Bush^2$ + Gr + GrHgt + SBstem	– 20.694	5	52.085	4.326	0.103	86.15	67.55
16-1	Bush + $Bush^2$ + Gr + GrHgt + Robel	– 25.198	5	61.093	13.334	0.001	77.14	60.94
16	Bush + $Bush^2$ + Gr + GrHgt	– 32.273	4	73.006	25.246	0.000	62.99	49.39

Table 2-11. Nest occurrence models and Akaike weights (w_i) for additional parameter models at the 1st radius (7.5-m scale) for 92 nests and 92 paired random locations based on the initial 2001-2003 AICc-selected top model (#36). Combinations of additional parameters only measured in 2001-2003 for Robel pole, sagebrush stem cover, and residual grass cover comprised candidate models. All model Likelihood Ratio (LR) χ^2 tests were significant at $P < 0.0001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	$\Delta_i AIC_c$	w_i	Model LR χ^2	% Dev. Explained
36-1	SBint + SBint^2 + Gr + GrHgt + Forb + ForbOth + Robel	– 36.419	7	88.171	0.000	0.717	54.70	42.89
36-5	SBint + SBint^2 + Gr + GrHgt + Forb + ForbOth + Robel + SBstem	– 36.419	8	90.572	2.401	0.216	54.70	42.89
36	SBint + SBint^2 + Gr + GrHgt + Forb + ForbOth	– 40.272	6	93.532	5.361	0.049	47.00	36.85
36-3	SBint + SBint^2 + Gr + GrHgt + Forb + ForbOth + SBstem	– 40.139	7	95.611	7.440	0.017	47.26	37.06

Table 2-12. Nest occurrence models and Akaike weights (w_i) for additional parameter models at the 2nd radius (15-m scale) for 92 nests and 92 paired random locations based on the initial 2001-2003 AIC_c-selected top model (#25). Combinations of additional parameters only measured in 2001-2003 for Robel pole, sagebrush stem cover, and residual grass cover comprised candidate models. All model Likelihood Ratio (LR) χ^2 tests were significant at $P < 0.0001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model LR χ^2	% Dev. Explained
25-3	SBint + Gr + SBstem	51.966	3	110.205	0.000	0.351	23.61	18.51
25-5	SBint + Gr + Robel + SBstem	51.086	4	110.631	0.426	0.284	25.37	19.89
25	SBint + Gr	53.679	2	111.492	1.287	0.184	20.18	15.82
25-1	SBint + Gr + Robel	52.630	3	111.533	1.328	0.181	22.28	17.47

Table 2-13. Estimated coefficients (β_i), standard errors (shown in parentheses), and 95% confidence intervals for top AIC$_c$-selected additional parameter nest occurrence models for all scales. Models were developed on only 92 of 93 nest and random locations in southeastern Alberta from 2001-2003. Observations were not recorded for one nest pair which was dropped. Added parameters are shown below the dashed line.

Variable	Nest Site Model 16-5	Confidence intervals		7.5-m radius Model 36-1	Confidence intervals		15-m radius Model 25-3	Confidence intervals	
		Lower	Upper		Lower	Upper		Lower	Upper
Bush	0.183 (0.083)	0.020	0.345						
[a]Bush^2	−0.183 (0.109)	−0.396	0.030						
SBint				0.822 (0.225)	0.380	1.263	0.366 (0.128)	0.114	0.618
[a]SBint^2				−2.721 (1.105)	−4.886	−0.556			
[a]Gr	−3.035 (3.133)	−9.176	3.106	−1.973 (2.755)	−7.372	3.427	4.022 (2.341)	−0.567	8.611
[a]GrHgt	4.355 (2.753)	−1.041	9.750	5.980 (4.057)	−1.970	13.931			
[a]Forb				−6.053 (6.781)	−19.343	7.238			
ForbOth				−0.321 (0.173)	−0.661	0.019			
Robel	0.104 (0.046)	0.014	0.193	0.127 (0.053)	0.023	0.230			
SBstem	0.266 (0.091)	0.087	0.444				0.260 (0.148)	−0.030	0.550

[a]Coefficients, standard errors, and confidence intervals for Bush^2, SBint^2, Gr, GrHgt and Forb have been multiplied by 100.

Table 2-14. Comparison of top AICc-selected nest occurrence models, metrics for overall model significance, model fit, and classification accuracy for the top model with additional parameters (measured for 93 nest and paired random locations from 2001-2003). All model Likelihood Ratio (LR) $\chi 2$ tests were significant at $P < 0.001$ (see previous five tables for scale specifics). Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model. The area under the receiver operating characteristic curves [ROC (SE)] and the percent correctly classified (PCC) based on the optimal cut off point were used to assess model classification accuracy. An independent sample with these measured parameters was not available, thus, classification statistics are show only for the training (model development) dataset.

Scale	Model	AIC_c-selected model		% Dev.	Model	Optimal	Training data	
	#		AIC_c	Explained	LR χ^2	cut-off	ROC	PCC
Nest site	16-5	Bush + $Bush^2$ + Gr + GrHgt + Robel + SBstem	47.246	72.74	92.77	0.5371	0.978 (0.008)	92.37
7.5-m radius	36-1	SBint + $SBint^2$ + Gr + GrHgh + Forb + ForbOth + Robel	87.474	42.89	54.70	0.5109	0.894 (0.022)	80.43
15-m radius	25-3	SBint + Gr + SBstem	110.205	18.51	23.61	0.5278	0.779 (0.034)	72.43

Table 2-15. AIC_c-selected proportional hazards nest survival models, Akaike weights (w_i) for all models comprising a cumulative summed AIC_c weights ($\sum w_i$) of ≥ 0.90 at the nest site (center quadrat) for 91 nests from 2001-2003. All model likelihood ratio (LR) χ^2 tests were significant at $P < 0.005$. K indicates the number of model parameters estimates. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	$\sum w_i$	Model LR χ^2	% Dev. Explained
22	Bush + $Bush^2$ + Forb + GrHgt	– 219.470	4	447.724	0.000	0.349	0.349	19.50	29.40
18	Bush + $Bush^2$ + Gr + Forb	– 219.544	4	447.872	0.148	0.324	0.673	19.35	29.22
20	Bush + $Bush^2$ +Gr + GrHgt + Forb	– 219.295	5	449.790	2.066	0.124	0.797	19.85	29.84
14	Bush + $Bush^2$ + Gr	– 222.337	3	451.135	3.411	0.063	0.860	13.76	21.79
16	Bush + $Bush^2$ + Gr + GrHgt	– 221.699	4	452.181	4.457	0.038	0.898	15.04	23.55
24	Bush + $Bush^2$ + Gr + GrHgt + Forb + ForbOth	– 219.282	6	452.278	4.554	0.036	0.933	19.87	29.87

Table 2-16. AIC$_c$-selected proportional hazards nest survival models, Akaike weights (w_i) for all models comprising a cumulative summed AIC$_c$ weights ($\sum w_i$) of ≥ 0.90 for the 7.5-m radius scale from the nest site for 91 nests from 2001-2003. All model likelihood ratio (LR) χ^2 tests were significant at $P < 0.005$. K indicates the number of model parameters estimates. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC$_c$	Δ_i AIC$_c$	w_i	$\sum w_i$	Model LR χ^2	% Dev. Explained
22	Bush + Bush^2 + Forb + GrHgt	– 218.108	4	445.001	0.000	0.310	0.310	22.22	32.75
20	Bush + Bush^2 + Gr + GrHgt + Forb	– 217.692	5	446.583	1.582	0.141	0.451	23.05	33.75
31	SBint + Gr + GrHgt + Forb	– 219.285	4	447.355	2.353	0.096	0.547	19.87	29.87
16	Bush + Bush^2 + Gr + GrHgt	– 219.824	4	448.433	3.432	0.056	0.603	18.79	28.50
7	SB + Gr + GrHgt + Forb	– 219.902	4	448.589	3.587	0.052	0.654	18.63	28.30
35	SBint + Gr + GrHgt + Forb + ForbOth	– 218.802	5	448.803	3.802	0.046	0.700	20.83	31.07
18	Bush + Bush^2 + Gr + Forb	– 220.024	4	448.832	3.830	0.046	0.746	18.39	27.99
33	SBint + Forb + GrHgt	– 221.222	3	448.906	3.905	0.044	0.790	15.99	24.84
24	Bush + Bush^2 + Gr + GrHgt + Forb + ForbOth	– 217.612	6	448.939	3.938	0.043	0.834	23.21	33.93
32	SBint + SBint^2 + Gr + GrHgt + Forb	– 219.142	5	449.485	4.484	0.033	0.867	20.15	30.22
11	SB + Gr + GrHgt + Forb + ForbOth	– 219.333	5	449.866	4.864	0.027	0.894	19.77	29.75
27	SBint + Gr + GrHgt	– 221.880	3	450.222	5.221	0.023	0.917	14.68	23.06

Table 2-17. AIC_c-selected proportional hazards nest survival models, Akaike weights (w_i) for all models comprising a cumulative summed AIC_c weights ($\sum w_i$) of ≥ 0.90 for the 15-m radius scale from the nest site for 91 nests from 2001-2003. All model likelihood ratio(LR) χ^2 tests were significant at $P < 0.001$. K indicates the number of model parameters estimates. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	$\sum w_i$	Model LR χ^2	% Dev. Explained
22	Bush + $Bush^2$ + Forb + GrHgt	− 217.347	4	443.479	0.000	0.432	0.432	23.74	34.56
20	Bush + $Bush^2$ + Gr + GrHgt + Forb	− 217.312	5	445.824	2.346	0.134	0.566	23.81	34.64
18	Bush + $Bush^2$ + Gr + Forb	− 218.718	4	446.219	2.741	0.110	0.676	21.00	31.27
16	Bush + $Bush^2$ + Gr + GrHgt	− 218.939	4	446.662	3.183	0.088	0.764	20.56	30.73
24	Bush + $Bush^2$ + Gr + GrHgt + Forb + ForbOth	− 217.025	6	447.764	4.285	0.051	0.814	24.39	35.31
32	SBint + $SBint^2$ + Gr + GrHgt + Forb	− 218.353	5	447.906	4.428	0.047	0.862	21.73	32.16
34	SBint + $SBint^2$ + Forb + GrHgt	− 219.582	4	447.948	4.469	0.046	0.908	19.27	29.12

Table 2-18. Estimated hazard ratios (exponentiated coefficients - exp[β_i]), standard errors (shown in parentheses), and confidence intervals for top AIC$_c$-selected candidate proportional hazards nest survival models in south-eastern Alberta across all scales for 91 nests from 2001-2003. Model 22 was the top AIC$_c$-selected model for all scales. Note: SBint, SBint^2, Gr, and ForbOth did not occur in the top model for any scale. Only at the nest site scale (Model 22-2, right of dashed line) did the top AIC$_c$-selected model change with the additional variables (see tables 2-21-2-23). Resid (below dashed line was the only additional variable in Model 22-2.

		Confidence intervals			Confidence intervals			Confidence intervals		Additional Variable	Confidence intervals	
Variable	Nest Site	Lower	Upper	7.5 m scale	Lower	Upper	15 m radius	Lower	Upper	Nest Site (Model 22-2)	Lower	Upper
Bush	0.954 (0.019)	0.917	0.993	0.935 (0.036)	0.866	1.009	0.918 (0.044)	0.835	1.009	0.958 (0.020)	0.920	0.998
[a]Bush^2	100.031 (0.026)	99.98	100.82	100.058 (0.111)	99.841	100.275	100.042 (0.155)	99.739	100.346	100.031 (0.026)	99.979	100.820
[a]GrHgt	99.696 (0.653)	98.42	100.98	98.020 (1.001)	96.077	100.002	97.913 (1.107)	95.768	100.106	99.269 (0.721)	89.692	100.56
Forb	0.994 (0.028)	0.890	1.001	0.937 (0.030)	0.881	0.998	0.956 (0.025)	0.909	1.006	0.950 (0.028)	0.897	1.006
Resid										1.027 (0.014)	1.001	1.054

[a]Coefficients, standard errors, and confidence intervals for Bush^2, GrHgt and have been multiplied by 100.

Table 2-19. Relative variable importance for proportional hazards nest survival models (2001-2003), based on the sum of the AIC_c weights for each variable across all models (91 nest sites). Sagebrush variables below the double line illustrate the strength of the measurement technique (quadrats vs. line intercept) and the importance of the quadratic relationship at each scale. Parameter Model Freq. indicates the frequency for each parameter occurring across all 23 models.

	Parameter Model Frequency	Nest Site	7.5-m scale	15-m scale
Bush + $Bush^2$	6	0.9334	0.6004	0.8295
SB	4	0.0107	0.0941	0.0160
SB + SB2	3	0.0029	0.0238	0.0060
Sbint	5	0.0401	0.2091	0.0188
Sbint + $SBint^2$	5	0.0130	0.0726	0.1297
Gr	20	0.6225	0.6064	0.5106
Grhgt	17	0.6101	0.9494	0.8743
Forb	13	0.8734	0.8444	0.8548
ForbOther	4	0.0432	0.1321	0.0684
All sagebrush (quadrats only)	7	0.0136	0.1179	0.0220
All sagebrush (intercept only)	10	0.0531	0.2817	0.1485
All sagebrush (linear)	9	0.0508	0.3032	0.0348
All sagebrush (quadratic)	8	0.0159	0.0964	0.1357
Any with sagebrush (both measurements)	17	0.0666	0.3996	0.1705

Table 2-20. Comparison of top AIC$_c$-selected nest survival models, Akaike weights (w_i), and metrics for overall model significance, fit, and classification accuracy for both training (91 nests from 2001-2003) and testing data (38 nests from 1998-2000) across all scales. All model likelihood ratio (LR) χ^2 tests were significant at $P < 0.001$ (see previous five tables for scale specifics). Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model. The area under the receiver operating characteristic curves [ROC (SE)] and the percent correctly classified (PCC) based on the training dataset optimal cut off point were used to assess model classification accuracy. Given that these are hazard survival models, predictions above the cut-off predict failure, below predict survival. Only at the nest site scale (shown below dashed line) did the top AIC$_c$-selected model change with the additional variables (see tables 2-21-2-23). An independent sample for additional variables was not available, thus, classification statistics are shown only for the training (model development) dataset.

Scale	Model #	AIC$_c$-selected model	AIC$_c$	Model LR χ^2	% Dev. Explained	Optimal cut-off	Training data		Testing data	
							ROC	PCC	ROC	PCC
Nest site	22	Bush + Bush^2 + Forb + GrHgt	447.724	19.50	29.40	0.2180	0.717 (0.055)	71.43	0.727 (0.082)	68.42
7.5-m radius	22	Bush + Bush^2 + Forb + GrHgt	445.001	22.22	32.75	0.2976	0.750 (0.053)	65.93	0.631 (0.096)	55.26
15-m radius	22	Bush + Bush^2 + Forb + GrHgt	443.479	23.74	34.56	0.2380	0.766 (0.050)	69.23	0.531 (0.106)	55.26
Additional Nest site Model 22-2	22-2	Bush + Bush^2 + Forb + GrHgt + Resid	446.496	23.14	33.85	0.2687	0.719 (0.054)	69.23		

Table 2-21. Proportional hazards nest survival models and Akaike weights (w_i) for additional parameter models at the nest site (center quadrat) for 91 nests based on the initial 2001-2003 AIC$_c$-selected top model (#22). Combinations of additional parameters only measured in 2001-2003 for Robel pole, sagebrush stem cover, and residual grass cover comprised candidate models. All model likelihood ratio (LR) χ^2 tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC$_c$	Δ_i AIC$_c$	w_i	Model LR χ^2	% Dev. Explained
22-2	Bush + Bush^2 + Forb + GrHgt + Resid	– 217.648	5	446.496	0.000	0.457	23.14	33.85
22	Bush + Bush^2 + Forb + GrHgt	– 219.470	4	447.724	1.228	0.247	19.50	29.40
22-4	Bush + Bush^2 + Forb + GrHgt + Robel + Resid	– 217.373	6	448.461	1.965	0.171	23.69	34.50
22-1	Bush + Bush^2 + Forb + GrHgt + Robel	– 218.949	5	449.097	2.601	0.124	20.54	30.70

Table 2-22. Proportional hazards nest survival models and Akaike weights (w_i) for additional parameter models at the 1st radius (7.5-m scale) for 91 nests based on the initial 2001-2003 AIC_c-selected top model (#22). Combinations of additional parameters only measured in 2001-2003 for Robel pole, sagebrush stem cover, and residual grass cover comprised candidate models. All model likelihood ratio (LR) χ^2 tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model LR χ^2	% Dev. Explained
22	Bush + $Bush^2$ + Forb + GrHgt	− 218.108	4	445.001	0.000	0.516	22.22	32.75
22-2	Bush + $Bush^2$ + Forb + GrHgt + Resid	− 217.754	5	446.709	1.707	0.220	22.66	33.60
22-1	Bush + $Bush^2$ + Forb + GrHgt + Robel	− 217.889	5	446.979	1.978	0.192	22.93	33.28
22-4	Bush + $Bush^2$ + Forb + GrHgt + Robel + Resid	− 217.606	6	448.926	3.925	0.072	23.23	33.95

Table 2-23. Proportional hazards nest survival models and Akaike weights (w_i) for additional parameter models at the 2nd radius (15-m scale) for 91 nests based on the initial 2001-2003 AIC$_c$-selected top model (#22). Combinations of additional parameters only measured in 2001-2003 for Robel pole, sagebrush stem cover, and residual grass cover comprised candidate models. All model likelihood ratio (LR) χ^2 tests were significant at $P < 0.001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC$_c$	Δ_i AIC$_c$	w_i	Model LR χ^2	% Dev. Explained
22	Bush + Bush^2 + Forb + GrHgt	−217.347	4	443.479	0.000	0.342	23.74	34.56
22-1	Bush + Bush^2 + Forb + GrHgt + Robel	−216.284	5	443.769	0.290	0.296	25.87	36.99
22-4	Bush + Bush^2 + Forb + GrHgt + Robel + Resid	−215.340	6	444.393	0.915	0.217	27.76	39.08
22-2	Bush + Bush^2 + Forb + GrHgt + Resid	−216.997	5	445.194	1.716	0.145	24.44	35.37

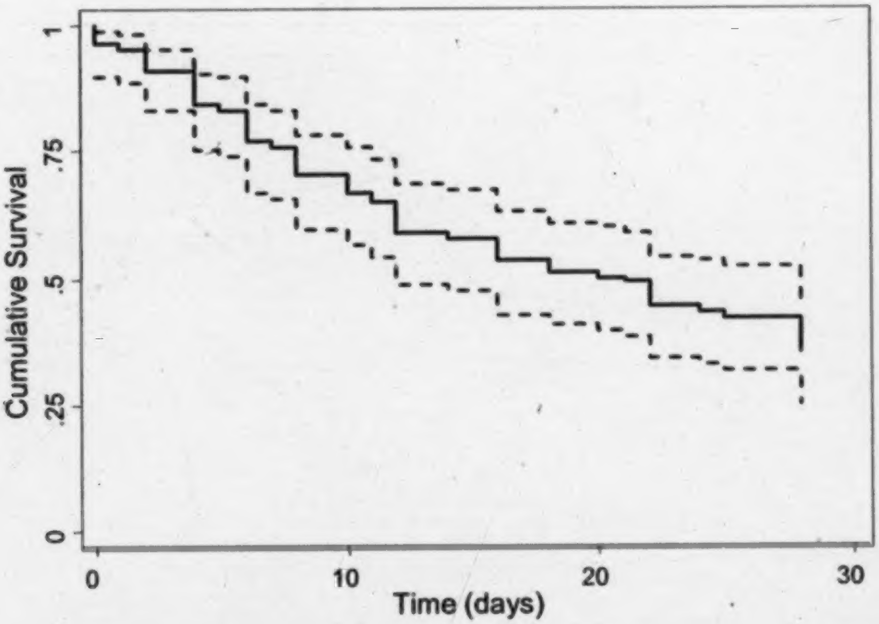

Figure 2-1. Kaplan Meier cumulative survival estimates and 95% confidence intervals for 91 sage-grouse nests during incubation in southeastern Alberta from 2001-2003. Six nests abandoned due to inclement weather events were right-censored.

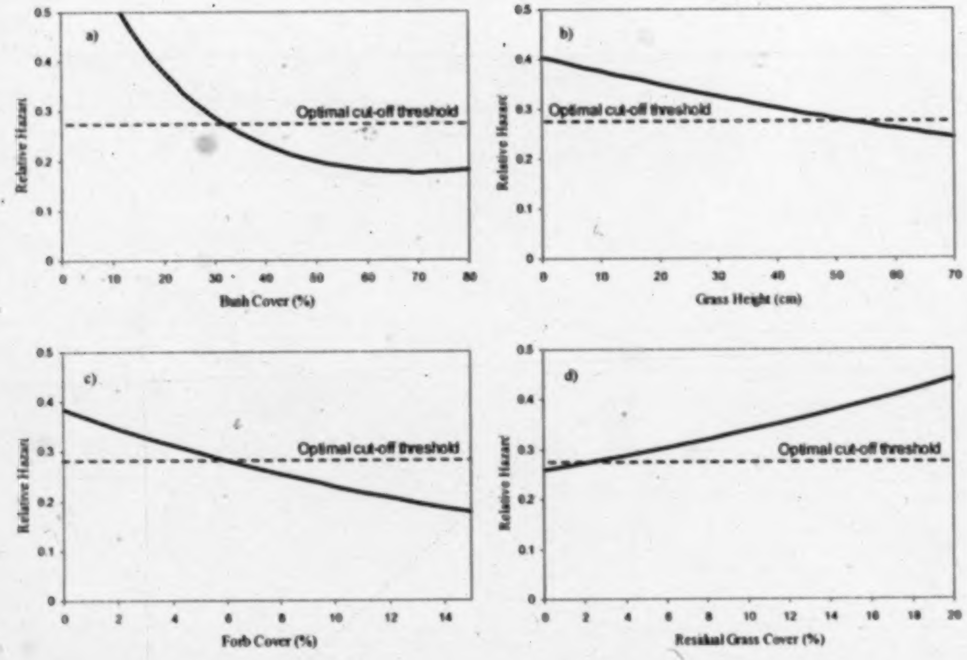

Figure 2-2. Threshold response curves for the top AIC$_c$-selected model (#22-2) at the nest site (center quadrat) for relative risk (hazard) of nest failure for sage-grouse nests in southern Alberta. Responses are shown across the 90th percentile of availability for each parameter in the model while holding the other parameters in the model at their mean values; a) bush, b) grass height, c) forb cover, and d) residual grass cover. Values below the optimal cut-off threshold (0.2687) indicate reduced hazard, and predicted nest survival.

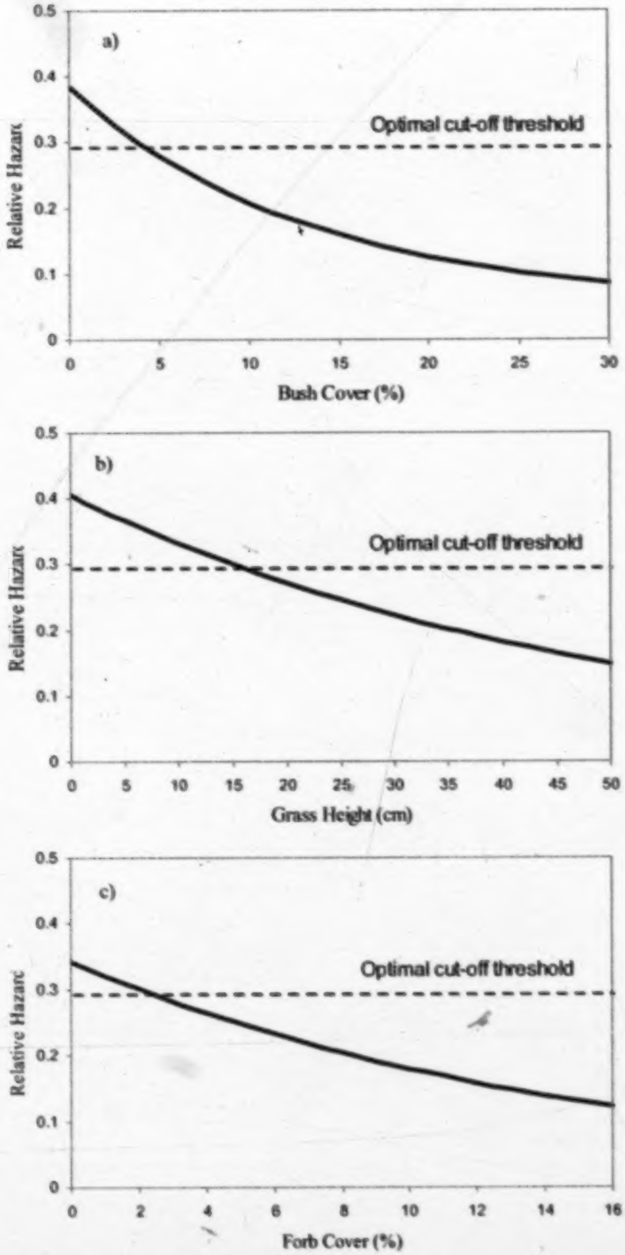

Figure 2-3. Threshold response curves for the top AICc-selected model (#22) at the 7.5-m radius for relative risk (hazard) of nest failure for sage-grouse nests in southern Alberta. Responses are shown across the 90th percentile of availability for each parameter in the model while holding the other parameters in the model at their mean values; a) bush, b) grass height, and c) forb cover. Values below the optimal cut-off threshold (0.2976) indicate reduced hazard, and predicted nest survival.

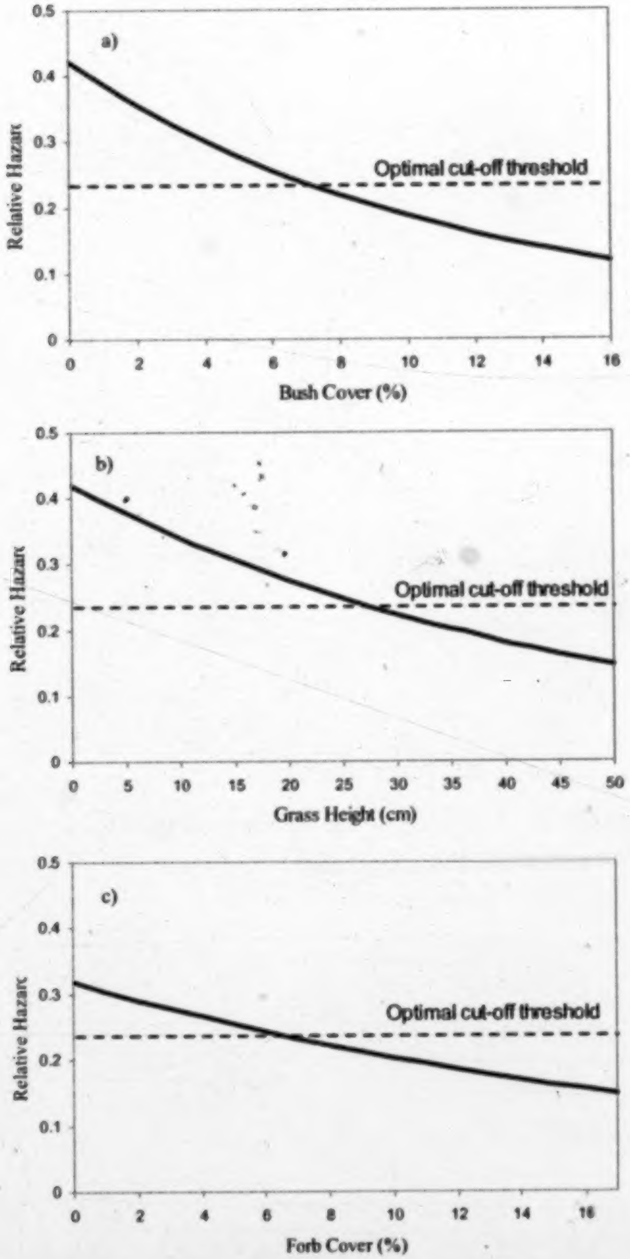

Figure 2-4. Threshold response curves for the top AIC_c-selected model (#22) at the 15-m radius for relative risk (hazard) of nest failure for sage-grouse nests in southern Alberta. Responses are shown across the 90th percentile of availability for each parameter in the model while holding the other parameters in the model at their mean values; a) bush, b) grass height, and c) forb cover. Values below the optimal cut-off threshold (0.2380) indicate reduced hazard, and predicted nest survival.

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Chapter Three

Greater Sage-Grouse Brood Habitat Selection and Chick Survival in Southeastern Alberta

1. Introduction

Greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') populations have experienced declines of 15-90% since the early 1970s (Connelly and Braun 1997; Connelly et al. 2004). Habitat conversion has resulted in a loss of more than 50% of habitats once occupied by sage-grouse (Schroeder et al. 2004), and currently occupied habitats continue to be degraded and fragmented (Braun et al. 2002; Crawford et al. 2004; Connelly et al. 2004). Reasons for population declines are not clear, but limited reproductive success (Connelly and Braun 1997; Braun 1998; Crawford et al. 2004) as a result of low nesting success (Crawford and Lutz 1985; Aldridge and Brigham 2001; Connelly et al. 2004) and poor chick survival (Aldridge and Brigham 2001; Burkepile et al. 2002) have been identified as potential drivers of declines and as management priorities.

Research has shown that mesic habitats with abundant forbs are selected as brood-rearing habitat by female sage-grouse (Klebenow and Gray 1968; Drut et al. 1994a; Sveum et al. 1998). The forbs and insects associated within these habitats (Johnson and Boyce 1991; Drut et al. 1994b) are important food resources necessary for chick survival. Sagebrush cover may also be important as brood rearing habitat with higher cover being selected in areas dominated by the less dense silver sagebrush communities (*Artemisia cana*; Aldridge and Brigham 2002) and lower cover selected in big sagebrush (*A.*

tridentata spp.) communities (Sveum et al. 1998). To date, however, no research on wild populations has assessed the links between chick survival and habitat use; research has only assessed habitat selection, or where broods occur (Crawford et al. 2004).

Chick survival is thought to be one of the most limiting demographic parameters for most prairie grouse (Aldridge and Brigham 2002; Aldridge and Brigham 2003; Connelly et al. 2004; Hagen et al. 2004). Correctly assessing chick survival, and identifying how to best manage habitats to ensure high recruitment is a priority outlined in most conservation and recovery strategies for sage-grouse range-wide (Harris et al. 2000; Connelly et al. 2004). In a recent synthesis paper summarizing sage-grouse ecology and management needs, Crawford et al. (2004) identify the lack of basic information on juvenile sage-grouse life history and habitat requirements as a management and research priority. To identify habitat requirements for chicks, assessing habitat selection (occurrence) alone may result in inaccurate assessments of habitat quality (Van Horne 1983; Morrison 2001) potentially leading to inappropriate management (but see Brock and Jones 2004). Thus, it is also necessary to assess how resources affect fitness (chick survival), if sound management recommendations are to be made.

Upland-game bird studies rarely mark and follow individual chicks, partly due to the difficulty in capturing and marking such small birds. As a result, monitoring brood survival using the brood as the sampling unit (Moynahan 2004), or using brood flush counts (Pitman 2003; Manzer 2004; Moynahan 2004) to estimate survival have been used as surrogates for chick survival. Brood counts could easily overestimate chick survival, because only one chick from a brood needs to be alive for the brood to be considered to have survived. On the other hand, brood flush counts could underestimate chick survival, because locating and flushing all chicks within a brood is difficult (Manzer 2004), particularly in thick vegetation.

The fate of individuals (chicks) within a cluster (brood) is not independent (Massot et al. 1994; Flint et al. 1995; Manly and Schmutz 2001). Methods used to avoid these biases include rarefying data to including only one individual per brood (Schroeder and Boag 1988; Massot et al. 1994), bootstrapping (Flint et al. 1995) to generate unbiased standard errors, or using maximum likelihood techniques that account for heterogeneity also allow for the assessment of covariate effects on survival (Manly and Schmutz 2001). These techniques are still not widely employed, and only the last approach produces both unbiased estimates in addition to appropriate standard errors for survival as well as model covariates. A less widely applied technique in the wildlife literature, which is easy to employ, is to estimate a latent random effect (Burnham and White 2002) for the cluster (brood), which enters multiplicatively on the survival or hazard function (Cleves et al. 2004). These models are referred to as shared frailty models and allow one to account for, and assess, correlation within groups (broods). Model parameter estimates are conditional on this shared frailty (Therneau et al. 2003; Cleves et al. 2004; Wintrebert et al. 2005), accounting for non-independence within the cluster (brood). Failing to account for this correlation will result in misspecified survival models with biased survival, parameter, and standard error estimates (Cleves et al. 2004).

Sage-grouse in Alberta have undergone severe population reductions, declining between 66-92% since the 1970s (Aldridge and Brigham 2001). This population has lost as much as 90% of its historic range (Aldridge and Brigham 2003). Remaining habitats are isolated from other populations and are heavily fragmented by oil and gas activities (Braun et al. 2002). Recent extended drought (Aldridge and Brigham 2003), and the introduction of the West Nile virus (Naugle et al. 2004) pose additional threats to the viability of this population. Productivity has been identified as a problem for this population (Aldridge and Brigham 2001, 2003), which may not be sustainable into the future unless long-term management initiatives improving habitat conditions are implemented (see Crawford et al. 2004).

My objectives were to first accurately assess chick survival in the Alberta sage-grouse population using a shared frailty proportional hazards modelling procedure. I compared these estimates from individually marked chicks to more traditional brood survival and flush count methods. Secondly, I assess 4th-order brood habitat requirements, developing occurrence models to identify important habitat characteristics selected by brooding female sage-grouse. I link habitat resources to survival using proportional hazards modelling at two spatial scales (patch and area), and include climatic covariates in this analysis. Finally, I use these models to identify habitat thresholds that can be used to direct management initiatives aimed at maintaining or enhancing critical brood-rearing habitat for sage-grouse in Alberta, as required by the Canadian Species at Risk Act (SARA).

2. Study area

The study area was located in the dry mixedgrass of prairie southeastern Alberta (49° 24' N, 110° 42' W, *ca* 900 m elevation). Daily summer (July-August) temperatures average 19.1°C and annual precipitation is *ca* 358 mm (AAFC-AAC 2004 unpublished weather data). This dry mixedgrass ecosystem is composed of many coulee draws and creeks with gentle slopes. There has been little conversion to cropland within this area, and silver sagebrush is the dominant shrub species. There is a variety of different forb species, including pasture sage (*A. frigida*), several species of clover (*Trifolium* spp. and *Melilotus* spp.), vetch (*Astragalus* spp.), and common dandelion (*Taraxacum officinale*). Needle-and-thread grass (*Stipa comata*), june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and western wheatgrass (*Agropyron smithii*) are dominant grass species (Coupland 1961, Aldridge and Brigham 2003).

3. Methods

3.1. Field techniques

Female sage-grouse were captured during the breeding season from 5 of 8 active leks in southeastern Alberta from 2001 – 2003 (see Chapter 2). Hens were fitted with a 14-g necklace-style radiotransmitter (RI-2B transmitters; Holohil Systems Ltd.; Carp, ON Canada). Nesting attempts and nest fate was assessed (see Chapter 2). If a nest was successful (i.e. ≥1 egg hatched), I relocated the radio-collared female using a 3-element Yagi antenna and an R-1000 scanning telemetry receiver (Communications Specialists, Inc. Orange, CA) and attempted to capture the chicks.

3.1.1. Chick captures and micro-transmitters

I captured chicks by hand as soon as possible after hatch, by triangulating the hen and flushing her from her brood (hens typically flushed only 20-30 m). Chicks averaged 2.5 days of age (range 0-8 days) at capture. I attached transmitters to 2 chicks randomly chosen from each brood. Transmitters weighed 1.6 g and had a battery life of 10-12 weeks (BD-2G transmitters; Holohil Systems Ltd.; Carp, ON Canada). I attached transmitters to chicks using two sutures similar to Burkepile et al. (2002).

Suture thread was fed through a sterile 20-guage needle inserted subcutaneously perpendicular to the chick's dorsal midline between the wings, leaving 5-10 mm of skin between needle insertion point and exit. The needle was removed and the anterior suture was fed through holes in the anterior of the transmitter and tied off with a gap of ~10 mm between the transmitter and the chick's body. I lined the bottom of the transmitter with a Skin Bond™ (Smith and Nephew Inc., Largo, FL) surgical adhesive to keep the transmitter tight to the midline. The transmitter was pressed gently up to the chick's midline, and the second suture was fed through the posterior holes and tied off, again with a gap of ~10 mm. All other captured chicks within a brood were weighed and received an individually numbered patagial wing tag. Handling of the entire brood took 15–45 minutes, depending on brood size; the attachment of transmitters took approximately 10 minutes each. Chicks were returned to the point of capture and remotely monitored via telemetry until the hen returned (usually within minutes). Chicks were monitored up to 8 weeks of age, as it is thought that at this age chicks can survive independently of their mother (Schroeder 1997; Schroeder et al. 1999). When possible, chicks that survived past this period were recaptured and transmitters removed. These techniques were originally developed as a pilot study at the University of Regina in 2000, where the technique was perfected on lay corn chicken chicks in captivity prior to application to 4 wild sage-grouse chicks (Aldridge 2000).

I relocated radio-collared hens and chicks every 2 days during the brood rearing period using standard telemetry techniques. If the signals indicated that hen and chick were no longer together, I located the chick to determine if it was alive. Signals were triangulated between 09:00 and 17:00, and birds were pinpointed from approximately 30-50 m away. This allowed me to estimate the exact position of the hen and chicks, which I recorded in Universal Transverse Mercator Coordinates using a hand held 12 Channel Global Positioning System (Garmin 12 XL and GPS II Plus; Garmin International Inc., Olathe, KS).

3.1.2. Habitat measurements

Once per week for each brood, I assessed the vegetation characteristics at a single brood location; typically two days after the brood was located. Brood site characteristics were measured similar to previous studies following the recommendations by Connelly et al. (2000, 2003). Measurements were taken at both the brood site location and a dependant random location using the same protocols outlined in Chapter 2. I estimated the percent cover of sagebrush, grasses, non-palatable forbs, palatable (to sage-grouse; Kerwin 1971) forbs, shrubs (other than sagebrush), and bare ground/dead materials within 1 m^2 quadrats, and mean maximum vegetation height for each cover class (see Chapter 2). I also measured sagebrush cover using the line intercept method (Canfield 1941). These same measurements were taken at brood locations from 1998-2000 by Aldridge and Brigham (2002), which I use as an independent sample for validating brood occurrence models (see section 3.2.4). I also estimated residual grass cover (Resid), vertical obstruction cover (Robel) using a Robel pole (Robel et al. 1970), and the percent litter cover (Litter, see Chapter 2).

3.1.3. Brood and chick survival

Once chicks were >21 days old, I flushed the hen and brood once per week and systematically searched within a 50-m radius of the flush location for any chicks that did not flush. I counted all chicks observed to estimate chick survival from flush counts. Hens that had lost their chicks typically flocked together with other broodless hens, or flew large distances when flushed (i.e., >300 m compared to 30 m when brooding). I continued to monitor hen behaviour every two days to confirm brood status. Brood failure was recorded as the first date I failed to detect chicks and no brooding behaviours were observed. When radio-marked chicks were not heard with the hen, I searched the area and that of the last known chick location for the signal, eventually searching the study area from a fixed-winged aircraft if signals could not be relocated. Date of death for a chick was estimated as the date the chick was not found with the hen. If chick signals could not be relocated, but the hen behaved as though she had lost her brood (i.e., flocked up), I considered the chicks to have failed on that date.

3.2. Data Analyses

I evaluated 4th-order (Johnson 1980) sage-grouse brood habitat selection and chick survival using a design IV approach, following individuals to identify a set of used resources with availability uniquely defined for each point of use (Erickson et al. 2001). My dependent random locations represent a random sample of unused units that I compared to used sites (brood locations) for occurrence modeling. While I never saw sage-grouse broods at random locations, I can not be certain that these locations were not used at other times in the season by broods. Thus, the unused sample truly represents a sample of 'available' points for occurrence modelling. Survival analyses were based solely on the use locations, comparing sage-grouse chicks that survived (0) to those that failed or died (1) over a particular interval.

I assessed brood habitat selection (occurrence) and chick survival at two scales surrounding the identified brood location. These scales were not originally biologically determined, but have been shown to be relevant to sage-grouse habitat selection (Aldridge and Brigham 2002). I analyzed vegetation characteristics within the 7.5-m area surrounding the brood relocation (177 m^2), hereafter referred to as the 'patch' scale, and within the 15-m area surrounding the brood location (707 m^2), hereafter referred to as the 'area' scale, following Aldridge and Brigham (2002). All analyses were conducted in STATA 8.2 (STATA 2004).

I obtained daily weather data from the Onefour Agriculture and Agri-food Canada Research Station located within my study area (AAFC-AAC 2004 unpublished weather data). I used these temperature and precipitation data to develop climate covariates with which I parameterize chick survival models.

3.2.1. Model development

My *a priori* candidate brood occurrence models were developed using data collected from 2001-2003 using the same set of variables that were also collected from 1998-2000 (Aldridge and Brigham 2002), with which I validated my models. I then attempted to improve the fit of my models using additional parameters I measured for the current training dataset [2001-2003; Robel (obstruction cover), Resid (residual grass cover), and Litter (dead fallen matter)]. Because I did not have chick survival data prior to 2001, candidate chick survival models included all habitat variables measured from 2001-2003, as well as climate variables. Given the small sample size of chicks, I was limited in the number of parameters I could model, and chose to evaluate the relative support for candidate models within three general hypotheses describing chick survival: 1) climate variables, 2) herbaceous and structural variables, and 3) sagebrush or shrub variables, before testing a candidate set of combined models, based on the top model within each of the above three groups.

I began model development by conducting univariate analyses for all predictor variables (Hosmer and Lemeshow 2000), and assessed models at both scales for outliers and non-linearities (Hosmer and Lemeshow 1999; Hosmer and Lemeshow 2000). I tested for collinearity between individual parameters i.e. r > |0.6| and tested for and multicollinearity using variance inflation factors (Menard 1995).

3.2.2. Matched case-control occurrence analyses

Similar to Chapter 2, I sampled habitats using a 1-1 matched case-control design (Hosmer and Lemeshow 2000:223; Manly et al. 2002:150), which constrains availability temporally and spatially, within similar range ecosite communities, controlling for factors that might lead to incorrect null models (Compton et al. 2002) or biases in habitat selection (Rosenberg and Mckelvey 1999). I generated resource selection functions (RSF) for paired observations using a case-control logistic regression following Manly et al. (2002:151):

$$\hat{w}(\mathbf{x}_{ij}) = \exp(\hat{\beta}_1 x_{ij1} + \hat{\beta}_2 x_{ij2} + \ldots\ldots + \hat{\beta}_p x_{ijp}) \qquad \text{(3-1),}$$

where $\hat{w}$ is the estimated relative probability for the *j*th resource unit being selected at the *i*th choice for the predictor variables, x_i, and the $\hat{\beta}_i$'s are the coefficient estimates for each predictor variable. Using this case-control logistic model with use-availability data allowed me to generate an RSF that is equivalent to the logistic discriminant between used and available locations, which is generally proportional to the probability of use (Manly et al. 2002; Keating and Cherry 2004). I present coefficients for occurrence models as unstandardized linear estimates and standard errors. I used the Huber-White sandwich variance estimator to inflate coefficient standard errors accounting for the lack of independence of repeated habitat samples for the same brood (Pendergast et al. 1996).

3.2.3. Proportional hazards survival analyses

Chicks were relocated on average every 2.3 ± 0.09 days, allowing me to estimate daily survival rates. I used a Kaplan-Meier (KM) product limit estimator (Kaplan and Meier 1958) with a staggered-entry design (Pollock et al. 1989; Winterstein et al. 2001) to estimate daily chick survival from hatch. I used a Log-rank χ^2 statistic (Winterstein et al. 2001) to test for differences in chick survival between years and between chicks hatched from initial or second nesting attempts. I did not have sufficient sample sizes to test for hen experience (1st year or experienced breeder) on chick survival. I compared KM chick survival estimates to KM brood survival estimated using the brood as the sampling unit. Broods were considered to have failed only when all chicks were lost. This is a commonly used surrogate for chick survival due to the difficulty in marking and following individual chicks within a brood (see Moynahan 2004).

To assess the effect of various habitat and climate covariates on chick survival, I used the Cox proportional hazards regression model (Cox 1972), which accommodates left and right censoring (Andersen and Gill 1982; Cleves et al. 2004). The Cox proportional hazards model estimates the hazard rate [$h\ (t|\mathrm{x}_i)$] for an individual ith subject as follows (Cleves et al. 2004):

$$h(t|\mathrm{x}_t) = h_0(t)\exp(\beta_{i1}x_{i1}+\beta_{i2}x_{i2}+\ldots\beta_{in}x_{in}) \quad (2\text{-}2),$$

where β_i's are the regression coefficients, x_i's are the covariates, and $h_0(t)$ is the baseline hazard, which is not parameterized and is left unestimated. I present coefficients for all survival models as hazard ratios ($\exp[\beta_i]$) and standard errors.

I compared the basic KM chick survival function to the baseline cumulative survival function without fitting any covariates, but fitting a latent random effect for chicks within broods. This allowed me to account for the lack of sibling independence and determine if the shared frailty model was necessary. I developed Cox proportional hazards models for each of my *a priori* candidate models using habitat (time varying) and climatic (some time varying and some fixed) covariates. Because I did not measure habitat characteristics at every two-day relocation (measured once per week), I had to assign habitat characteristics across intervals with no measurements. Johnson et al. (2004) found that parameters used in grizzly bear (*Ursus arctos*) survival models were robust, whether habitat covariates were aggregated forward or backwards across intervals. Thus, I carried forward habitat covariates across intervals, assuming exposure was constant until the subsequent weekly habitat measurement location. Nest habitat characteristics (Chapter 2) were used as the initial habitat characteristics chicks were exposed to. I had independent climate variables (see section 4.1.2 below) for each interval.

Deaths with tied failure times were partitioned using the Breslow estimation of the continuous-time likelihood calculation (Cleves et al. 2004). For each of my candidate models, I assessed the proportional hazards assumption (Winterstein et al. 2001), which assumes that the effects of the covariates on survival do not change over time, except for ways in which the model is already parameterized (Cleves et al. 2004). Logarithm quadrats of the estimated cumulated hazard functions that were not parallel, or quadrats of Schoenfeld residuals suggesting a non-zero slope indicated violations of the proportional hazards assumption (Andersen and Gill 1982; Schoenfeld 1982; Cleves et al. 2004). I also used a χ^2 goodness-of-fit test on the Schoenfeld residuals to statistically test for a non-zero slope (Grambsch and Therneau 1994; Cleves et al. 2004). I report survival estimates as means ± standard errors.

3.2.4. Model selection, assessment and validation

I chose to use an information-theoretic approach to model selection using Akaike's Information Criteria (AIC) with a correction for small sample size (AIC_c; Anderson et al. 2000; Burnham and Anderson 2002). For the case-control logistic occurrence models, the sample size is the number of paired groups. The Cox proportional hazards models are essentially a conditional logistic model (Cleves et al. 2004). Thus, sample size is the number of events or chick deaths/failures (Cleves et al. 2004). AIC_c values were calculated for my frailty models including the theta (θ - frailty variance) as an estimated parameter (Burnham and White 2002). For both analyses, I used the differences in AIC_c scores (Δ_i) to identify the best approximating occurrence or survival model within the candidate set (i.e., most parsimonious model with the best explanatory power; Anderson et al. 2000; Burnham and Anderson 2002)] and AIC_c weights (w_i) to assess the probability that a given model was the best within the candidate set (Anderson et al. 2000; Burnham and Anderson 2002). I also assessed the relative variable importance by summing the AIC_c weights across all models.

I used a Wald χ^2 statistic (Hosmer and Lemeshow 2000) to asses the fit of each survival or occurrence model to the data and estimated the variance explained by calculating reduction in log-likelihood for the given model from the null model (deviance explained). For survival models, I compared the 'relative' deviance estimates between survival models within the same candidate set, as outlined by Hosmer and Lemeshow (1999).

I assessed the effect of parameters on the top AIC_c-selected survival and occurrence model at each scale using 95% confidence intervals. Occurrence model coefficients that did not overlap zero (0 = no effect) had strong effects on habitat selection. Given that I report survival model coefficients as hazard or risk ratios, coefficients that did not overlap 1 (1 = no hazard) contributed to the survival model.

I did not use model averaging (Burnham and Anderson 2002) with my combined sagebrush/shrub parameters modelled (see Chapter 2 for detailed explanation). Although I only present coefficient estimates for top models at each scale, I discuss the similarity of coefficients across all candidate models, which, if largely consistent, alleviate the need to model average (Burnham and Anderson 2002:150).

For occurrence models, I predicted the top case-control logistic models on my dataset using a logistic equation. I used receiver operator characteristic (ROC) estimates (Fielding and Bell 1997) to assess the predictive accuracy of top AIC_c-selected occurrence models using the following guidelines: estimates above 0.9 indicate high model accuracy; estimates between 0.7 to 0.9 indicate good model accuracy; values below 0.7 indicate low model accuracy (Swets 1988; Manel et al. 2001). I used the percent correctly classified (PCC) at the optimal cut-off to estimate the predictive capacity of the top occurrence models. PCC ≥ 80% was considered as excellent prediction and PCC ≥ 70% was considered reasonable model prediction (Nielsen et al. 2004). I validated top models with an independent sample of 113 brood locations collected from 1998-2000 for 17 different broods (see Aldridge and Brigham 2002) by predicting models on this new dataset and assessing fit and prediction as described for model training datasets. Predicted probabilities above the optimal probability cut-off point (point that maximized both the sensitivity and specificity curves; Swets 1988; Nielsen et al. 2004) as presence, and probabilities below the cut-off as absences.

To assess the fit of the top combined AIC_c-selected chick survival models, I predicted cumulative hazard using the top model at each scale and tested for differences in daily relative hazard for chicks that failed (1) compared to those that survived (0). If the model was predictive, chicks that died should have a greater daily hazard than those that survived. I tested this hypothesis using a *t*-test with unequal variances. Finally, I developed predictive survival curves for top combination models to assess the risk of chick failure across a range of values for each parameter in the model. I varied the parameters of interest across 90th percentile of the range of availability for that parameter, while holding all other parameters at their mean values. This allowed me to generate dose response curves and identify threshold levels for the relative hazard or risk of chick failure in relation to each parameter of interest. I could not generate similar dose response curves for occurrence models due to the conditional nature of the case-controlled analyses.

4. Results

During the three years of my study (2001-2003) I was able to track 24 broods, for which I conducted vegetation measurements at 139 brood sites; 42 sites from 8 broods in 2001; 15 sites from 3 broods in 2002; 82 sites from 13 broods in 2003. Brood numbers were low in 2002 due to extreme spring weather events that resulted in fewer nests hatching (see Chapter 2). I measured habitat characteristics at an average of 5.8 ± 0.86 sites for each brood. Three females produced broods in 2 different years and I retained both broods for my occurrence analyses.

Of these 24 broods, I captured a total of 130 chicks from 23 broods (I did not capture chicks from 1 brood), and radio-marked 41 chicks from 22 different broods to assess chick survival. At capture (2.5 days of age, range 0-8 days) chicks averaged 34.4 ± 0.6 g (n=130). Thus, micro-transmitters (1.6 g) were < 5% of chick mass at initial capture. I obtained an average of 11.0 (range 1-43) relocations per chick. One chick death was research related and this individual was censored on the death date. For 2 chicks that moved with hens onto lands that I did not have permission to access, I right censored them on the date of their last known observation. Two other chicks died of non-predation events; one chick fell down a hole and died, and one died of exposure (drowned) after flooding from a summer rain storm. These chicks were right censored at their last known alive location, and I modelled chick failure due to predation events only.

4.1. Candidate models

Sagebrush cover estimated by either the quadrat method (SB) or Canfield line intercept method (SBint) were positively correlated ($r > 0.70$) at both scales. Thus, only one measure of sagebrush cover was used in competing models. Because sage-grouse have been shown to select for overall shrub cover (Aldridge and Brigham 2002), at least for nesting (see also Chapter 2), I estimated an overall shrub canopy estimate called 'Bush', which was the combination of other shrubs and sagebrush canopy cover from the quadrats. I used Bush as a third shrub component variable (Table 3-1).

Grass height was the only vegetation height measure that was not correlated with its respective cover measure ($r < 0.55$; for other variables, $r > 0.76$). All other correlated height variables were less predictive than cover estimates (based on deviance) and I retained cover measures for inclusion in my *a priori* candidate models. I retained grass height as a candidate variable, and height was considered to be zero for all measurements when no grass was present (i.e., 0% cover). All shrub and herbaceous variables used in candidate models, and means for use and random locations are shown in Table 3-1.

4.1.1. Occurrence candidate models

I felt that sage-grouse hens may select for moderate ranges of sagebrush/bush cover at brood habitat (concave function or inverted U shape), because very thick shrub cover can limit herbaceous understory and might reduce the birds ability to detect predators (Wiebe and Martin 1998). Thus, in addition to testing a positive linear relationship for each shrub component variable (SB, SBint, Bush), I also fit a quadratic relationship for each (positive but decreasing function), arriving at six different shrub component variables (Table 3-2a). All six shrub component variables were combined with six different herbaceous variable combinations (Table 3-2a), resulting in 36 different *a priori* candidate models for sage-grouse brood occurrence (Table 3-2b). I only present results for the top occurrence models that represent the 90% confidence set ($\sum w_i > 0.90$).

Additional parameters measured in 2001-2003 included visual obstruction cover (Robel), residual grass cover (Resid), and litter ground cover (Litter; Table 3-1). I re-evaluated the top model at each scale with the addition of these variables (six additional model combinations; Table 3-3). Residual grass (Resid) was not correlated with grass cover ($r < 0.60$) at either scale, allowing the inclusion of both grass cover and residual grass cover in additional parameters models (Table 3-3).

4.1.2. Survival candidate models

Given the small sample size for chick survival models, and my choice to model climatic, shrub, and herbaceous components, I was forced to keep the models fairly simple. Thus, I chose to first identify the top candidate models within three groups of predictor variables separately (climate, shrub vegetation, and herbaceous vegetation), and then combine the top model from each group to develop my final candidate set of models. I examined seven different univariate climate models (Table 3-4), consisting of various cumulative growing degree day and precipitation measures. Cumulative growing degree days was estimated as the number of degrees above 5°C for each mean daily temperature (Ball et al. 2004), summed over the growing season (from 1- March to the given date of that year; Table 3-4). I calculated several precipitation measures, and finally, a dryness index (Dry_index), which was the growing degree days for that year (GDD) divided by the cumulative spring precipitation since the beginning of the growing season (01-March, Sp_PPT_Cumm; Table 3-4). The GDD model by itself violated the proportional hazards assumption (χ^2 goodness-of-fit test of the non-zero slopes, $P < 0.05$), and was dropped from further analyses.

The same six shrub variables used for the brood occurrence analyses were used for shrub chick survival models as a separate candidate set to identify the best model (Table 3-5). I had 13 different 1 to 2 parameter herbaceous component models (Table 3-5), which I also initially assessed as a separate candidate set. Model 12 violated the proportional hazards assumption (χ^2 goodness-of-fit test of the nonzero slopes, $P < 0.05$) and was dropped from the candidate set. Once I identified the top survival models for each group (see below) I developed a new candidate model set with combinations of these top models.

4.2. Conditional fixed-effects occurrence analyses

Top brood occurrence models at both scales had weak support ($w_i < 0.90$) for my original 2001-2003 training dataset models (Tables 3-6, 3-7), but coefficient (β_i) estimates were consistent across all candidate models (only top models shown in Tables 3-8 to 3-10). Similar trends were seen for the additional parameters models, but again, coefficients were consistent (Tables 3-11, 3-12). Thus, I did not model average coefficients and discuss the patterns based on coefficients for the top-selected model at each scale.

4.2.1. Patch scale brood occurrence

None of the top candidate ($\sum w_i > 0.90$) models at patch scale contained the Bush variable (Table 3-6). All ten top models contained sagebrush cover (SB) estimated with the quadrat method, with the top two models including a quadratic term. All models were highly predictive, explaining about 50% of the variation in brood occurrence (Table 3-6). Model #10 was the top AIC$_c$-selected brood occurrence and had good fit (Wald $\chi^2_4 = 43.96$, $P < 0.0001$) but had weak support ($w_i = 0.16$) within my candidate set of models.

This model however, had great accuracy when predicted on both the training and validation datasets ($ROC_{train} = 0.992$, $ROC_{test} = 0.841$, Table 3-10) and excellent prediction (84.1%) for the training dataset, and good prediction when validated on the testing dataset (77.0%, Table 3-10).

Inferences based on this top model indicate strong positive but decreasing selection for sagebrush cover ($\beta_{SB} = 0.460 \pm 0.083$, $\beta_{SB2} = -0.007 \pm 0.001$; concave function; Table 3-8). Hens selected strongly for taller grass cover ($\beta_{GrHght} = 0.058 \pm 0.025$) at brood sites, but only weakly for greater forb cover ($\beta_{Forb} = 0.038 \pm 0.021$; Table 3-8). Overall, there was strong weight of evidence for selection of sagebrush (combining all measures of sagebrush, $\sum w_i = 1.00$), and sagebrush estimated with the quadrat method (SB) had the strongest support ($\sum w_i = 0.94$; Table 3-9) of the various measures. Despite the fact that the quadratic relationship for sagebrush occurred in the two top models, variable importance weights indicated there was minimal support for the quadratic relationship with sagebrush cover (quadratic relationship, $\sum w_i = 0.56$) over a linear relationship indicating selection for maximum cover ($\sum w_i = 0.44$; Table 3-9). Grass height also had strong support ($\sum w_i = 0.91$). Despite Grass occurring in only 6 models it had moderate support ($\sum w_i = 0.70$), as did Forbs ($\sum w_i = 0.66$).

Adding the additional parameters to the top model (#10) only increased the variance explained in brood-site selection at the patch scale by <1 % (Table 3-11). Not surprisingly, the base model remained the top model still with only moderate support ($w_i = 0.36$). Thus, I restricted my inference about patch scale brood site selection to this more parsimonious base model (see Table 3-9).

4.2.2. Area scale brood occurrence

Again, none of the top candidate ($\sum w_i > 0.90$) models at patch scale contained the Bush variable (Table 3-7). However, the 8 top models within this 90% confidence set contained the SBint variable as a linear or quadratic (SBint + SBint^2) term, and all contained the GrHgt variable (Table 3-7). All models explained >41% of the variation in brood habitat selection with the top model (Model 28) explaining 44.1% (Table 3-7). Similar to the patch scale, this top model had weak support ($w_i = 0.18$) as the top candidate model, but had good fit (Wald $\chi^2_4 = 56.42$, $P < 0.0001$) and good model accuracy for both training and validation datasets ($ROC_{train} = 0.900$, $ROC_{test} = 0.802$, Table 3-10). This model had good prediction (79%) for the training dataset and reasonable prediction on the independent testing dataset (71%, Table 3-10).

Inference based on the top model (Model #28) at the area scale again indicated strong positive but decreasing selection for sagebrush cover ($\beta_{SBint} = 0.757 \pm 0.170$, $\beta_{SBint2} = -0.024 \pm 0.008$; concave function; Table 3-8). Hens selected strongly for taller grass ($\beta_{GrHght} = 0.115 \pm 0.028$) at brood sites, but avoided areas with greater grass cover ($\beta_{Grass} = -0.040 \pm 0.011$; Table 3-8). Overall, there was again strong evidence of support for selection of sagebrush (any sagebrush measure, $\sum w_i > 0.99$), but models estimated with the line intercept (SBint) had stronger support ($\sum w_i = 0.74$) than for the quadrat method ($\sum w_i = 0.26$; Table 3-9). Again, models with moderate-to-high sagebrush cover (quadratic relationship, $\sum w_i = 0.57$) only had minimal support over selection for maximum sagebrush cover (sagebrush univariate linear relationship ($\sum w_i = 0.42$). Both GrHgt ($\sum w_i = 0.99$) and Grass ($\sum w_i = 0.83$) had strong evidence of support, and Forbs ($\sum w_i = 0.60$) had moderate support.

Similar to the patch level brood occurrence models, adding additional parameters to the top AIC_c-selected model #28, resulted in only minor improvements in the variance explained (< 2%) in brood site selection at the area scale (Table 3-12). The base model again remained the top model with weak support ($w_i = 0.23$). However, I again restricted my inferences about area-scale brood site selection to this most parsimonious base model #28 (see Table 3-9).

4.3. Proportional hazards survival analyses

Chick survival to 8 weeks (56 day) estimated using a basic Kaplan Meier curve was 29.6 ± 8.10% (Figure 3-1). KM brood survival produced a somewhat similar survival curve (Figure 3-1), but survival to 56 days (63.4 ± 10.49%) was over twice the basic KM chick survival estimate. There were no differences in survival between years (Log rank $\chi^2_2 = 2.86$, $P = 0.24$), but sample sizes by year were small (14 chicks in 2001, 4 chicks in 2002, 23 chicks in 2003). There was also no survival differences between chicks hatched from first nesting attempts (n = 33) and second nesting attempts (n = 8; Log rank $\chi^2_1 = 2.32$, $P = 0.13$). Thus, I combined all chicks for further survival analyses using habitat and climatic covariates.

The baseline hazard chick survival model using the shared frailty to account for the lack of independence of chicks within the same brood resulted in lower survival estimates (Figure 3-2). Chick survival to 56 days estimated with the baseline shared frailty model (12.3%, Figure 3-2) was lower than that estimated with the basic fixed effects KM curve (29.6%), and was outside the 95% CI for the KM model (range 15.1 to 49.7%, Figure 3-2). The estimate of the frailty variance ($\theta = 0.96$) was quite large and was significant at $\alpha = 0.10$ for the baseline survival model (Likelihood ratio $\chi^2_1 = 1.87$, P

= 0.086), suggesting that I needed to account for the correlation among the predicted survival of chicks within broods. Thus, I fit the shared frailty model for all candidate models, even if model covariates within the specific model explained some of the within group variation resulting in small variance (θ) estimates.

For comparison with other studies that assessed survival to 30 days, survival to 30 days in my study was 43.25% for the KM model, and 29.6% for the shared frailty model. Brood survival to 30 days was 63.3% and no broods completely failed (lost all remaining chicks) between 30-56 days. Similarly, chick survival estimated based on brood flush counts at 30 days was 16.25% (estimated from 160 hatched eggs from 19 broods) and 12.9% at 56 days (estimated from 155 hatched eggs from 18 broods – 1 brood was censored).

4.3.1. Climate chick survival models

Of the six climate models I tested, the dryness index was the top AIC$_c$-selected model (Table 3-13). This model had only moderate support ($w_i = 0.34$), but had reasonable fit to the data (Wald $\chi^2_1 = 3.48$, $P = 0.06$). By itself, the dryness index explained more that twice as much variation in chick survival than any other climate variable (10.97%; Table 3-13). Thus, I used this top climate model #3 (Dry_Index) for my combined models.

4.3.2. Shrub chick survival models

At the patch scale, the top AIC$_c$-selected chick proportional hazards shrub model contained the SB variable, suggesting a linear relationship with chick survival (Table 3-14). This model (#1) had only moderate support ($w_i = 0.44$), but the Akaike weight was more than double the second best model (SBint; Table 3-14). The model had significant fit to the data (Wald $\chi^2_1 = 6.13$, $P = 0.01$), explained 14.22% of the variation in chick survival, and was used for combined candidate model building.

At the area scale, the top AIC$_c$-selected chick proportional hazards model contained the quadratic for sagebrush (SBint + SBint^2), estimated with the line intercept method (Table 3-14). This model had moderate support ($w_i = 0.34$) and the Akaike weight was about twice that of the next best model (Table 3-14). This model had good fit to the data (Wald $\chi^2_1 = 6.09$, $P < 0.05$) and explained the most variation within the candidate set at this scale (22.56% deviance explained, Table 3-14). Thus, I used shrub model #6 (SBint + SBint^2) for combined candidate models.

4.3.3. Herbaceous chick survival models

At the patch scale, model #8 (Gr + GrHgt) was the top AIC$_c$-selected herbaceous survival model (Table 3-15). This model had weak support ($w_i = 0.30$) and moderate fit to the data (Wald $\chi^2_1 = 4.76$, $P = 0.09$), but explained the greatest deviance (18.53%) of all herbaceous models (Table 3-15). At the area scale, model #8 was again the top AIC$_c$-selected herbaceous survival model (Table 3-15). This model had poorer fit to the data (Wald $\chi^2_1 = 3.70$, $P = 0.16$) and again had weak support ($w_i = 0.20$), but also explained the greatest deviance from the null model (14.35%; Table 3-16). Thus, for both the patch and area scales, I used model #8 (Gr + GrHgt) as the herbaceous model for combined candidate models.

4.3.4. Combination chick survival models

Using the top shrub and herbaceous models at each scale and the top climate model, I developed seven candidate models for each scale tested. The candidate model set consisted of the top models from each group and all possible combinations of these models (see Table 3-17). At the patch scale, the combination of the top climate and shrub models (SB + Dry _Index) failed to converge on a maximum likelihood estimation, and could not be parameterized. Thus, I dropped this model from both scales, resulting in six candidate models for the combined analyses (Table 3-17).

Model #5 was the top AIC_c-selected model at the patch scale, containing a climate and herbaceous component (Table 3-18). This model had good fit (Wald $\chi^2_1 = 12.12$, $P = 0.007$), moderate support ($w_i = 0.65$) and explained 42.68% of the variation in chick survival (Table 3-18). Model #6 was the second-ranked model, and differed only from the top model in the addition of the SB parameter to the top model. This second-ranked model had smaller Akaike weight ($w_i = 0.15$), but explained a similar amount of variation (43.30%). Parameters common to these two models were virtually identical, and I chose to make inferences using the more parsimonious top-ranked model. Risk of chick failure increased as the drought index increased ($\beta_{Dry\_Index} = 1.44 \pm 0.184$, Table 3-19). Although risk of chick failure was strongly reduced with increased grass cover ($\beta_{Gr} = 0.932 \pm 0.026$, Table 3-19), tall grass had the opposite effect ($\beta_{GrHgt} = 1.056 \pm 0.021$, Table 3-19); risk increased as grass height increased. Not surprisingly, Gr, GrHgt and Dry_Index all had strong variable importance weights ($\sum w_i > 0.85$; Table 3-20).

Threshold response curves developed based on patch scale model #5 suggested a significant reduction in risk to sage-grouse chicks if grass cover is greater than 20-25% (Figure 3-3a). Although risk increased with increasing grass height (i.e. $\beta_{GrHgt} > 1.0$, Table 3-19), the model illustrates that this risk is evident only when grass is greater than *ca* 40 cm in height (Figure 3-3b). The model also clearly illustrates that the moderate-to-high dryness index values dramatically increase the risk of chick death (Figure 3-3c).

Model #6 was the top AIC_c-selected model at the area scale (Table 3-18). This model had good fit (Wald $\chi^2_1 = 16.74$, $P = 0.005$), strong support as the top candidate model in my given combined set ($w_i = 0.91$), and explained considerably more variation in chick survival (58.27%) than any other model (Table 3-18). At this scale, there was also high risk of failure as the dryness index increased ($\beta_{Dry\_Index} = 1.707 \pm 0.268$, Table 3-19). Risk of failure was positive but decreasing with sagebrush cover ($\beta_{SBint} = 2.068 \pm 0.549$, $\beta_{SBint2} = 0.941 \pm 0.022$; Table 3-19), suggesting higher chick survival in less dense sagebrush habitats. Risk of chick failure was slightly reduced with increased grass cover ($\beta_{Gr} = 0.953 \pm 0.031$, Table 3-19), and again, risk increased as grass height increased ($\beta_{GrHgt} = 1.076 \pm 0.027$, Table 3-19). All variables had strong variable importance weights ($\sum w_i > 0.94$; Table 3-20), suggesting they were all important for chick survival.

Threshold response curves for the area scale using model #6 indicate that the relative risk of chick death increased with greater sagebrush cover, and tailed off in more dense sagebrush habitats (Figure 3-4a). Risk appeared to be high above about 3% sagebrush cover (line intercept method) but reduced if cover was greater than about 9% (inverted U shape). Similar to the patch level threshold curves (Figure 3-3a), risk was reduced with increased grass cover at the area scale, but the threshold was lower (> 5% cover, Figure 3-4b). Risk also increased with increasing grass height at the area scale, but only when grass was taller than about 30-35 cm (Figure 3-4c). Again, the area-level-threshold model also illustrates that hot and dry growing seasons (high dryness index values) will result in reduced chick survival (Figure 3-3d).

Both the patch and area scale models validated well on the within-sample testing dataset. The mean daily hazard was significantly greater for chicks that died within the

56 day monitoring period compared to those that survived or were censored (patch scale: $t_{37.2} = 4.17$, $P < 0.001$; area scale: $t_{31.9} = 3.73$, $P < 0.001$). Thus, as should be expected if my model was predictive, I show that chicks that died were exposed to more hazardous or risky conditions, based on my model covariates.

5. Discussion

Survival of sage-grouse chicks to 56 days was only 12.3% using my shared frailty model. Burkepile et al. (2002) using the same micro-transmitter technique for greater sage-grouse chicks in southeast Idaho estimated apparent chick survival to 21 days between 21-32 %. Similarly, for sharp-tailed (*Tympanuchus phasianellus*) grouse in Alberta, Manzer (2004) found 41% of chicks survived (KM estimate) to 30 days of age using this micro-transmitter technique. Estimated from the basic KM function, chick survival in my study to 30 days (43.25%) was comparable to these studies, but after accounting for the lack of independence between chicks within the same brood, my shared frailty KM estimate of survival was considerably lower (29.6% at 30 days). Manzer (2004) used bootstrapped SEs to account for correlation of sharp-tailed grouse chicks within broods (Flint et al. 1995) which appropriately inflated the SEs, but, as the frailty model illustrates, the survival estimate may be biased. I advocate that researchers estimating survival with correlated individuals within clusters (e.g., broods or litters), fully investigate this lack of independence and account for it using latent random effects (Therneau et al. 2003; Cleves et al. 2004; Wintrebert et al. 2005), such as the shared frailty modelling approaches I applied here.

Although I did not have an alternative sample of marked and resighted chicks to compare with survival of radio-marked chicks, the fact that chick survival estimated from flush counts was lower at 30 days (16.25%) but similar at 56 days (12.9%), and given that transmitters were < 5% of chick body weight at capture, I feel comfortable that radiotransmitters had minimal effect on overall survival of chicks. However, the low flush count estimates at 30 days may be a result of my inability to locate all chicks within a brood, particularly in areas with thicker vegetation. My findings closely mirror Manzer's (2004) research on sharp-tailed grouse, where flush counts at 30 days resulted in chick survival estimates 1.6 times lower than KM estimates for radio-marked chicks. However, the larger size of chicks at 56 days of age in my study might have made chicks more visible, and thereby easier to locate and flush, resulting in flush count survival estimates similar to those based on radio-marked chicks. A previous study in Alberta using flush counts found comparable chick survival estimates of *ca* 18% to 43-50 days of age (Aldridge and Brigham 2001). Thus, there may be some merit in using flush counts to estimate chick survival, particularly once chicks are older and more easily located. This relationship needs to be explored further with a larger sample of marked and unmarked chicks.

Using the brood (minimum one chick surviving) as the sampling unit resulted in survival estimates that were over 5 times the KM shared frailty chick survival estimate at 56 days of age (63.3% vs. 12.3%, Figures 3-1, 3-2). Brood survival to 30 days (66.3%) was similar to estimates (69%) from a recent study in a large population of sage-grouse in Montana (Moynahan 2004). However, as with chick flush count estimates, I caution against the use of these estimates as surrogates for chick survival, particularly when assessing demographic parameters in life stage simulation type of analyses (Wisdom et al. 2000) using sensitivity and elasticity analyses. Failure to appropriately estimate and incorporate individual chick survival into demographic analyses may result in the inappropriate identification of important parameters, misguiding management. Also, using broods as a surrogate for chicks might mask the importance of certain habitat covariates when modelling survival. I encourage further comparative research.

My proportional hazards survival models using climatic and habitat (shrub and herbaceous) covariates had good predictive power, explaining 42.7 % and 58.3 % of the variation in chick survival at the patch and area scales, respectively (Table 3-18). The dryness index played a strong role in predicting chick survival, occurring in top models at both scales (Figures 3-3, 3-4). Hot, dry years with little precipitation during the spring and summer strongly increase the risk of chick failure. Spring precipitation has long been suggested to be correlated with sage-grouse productivity (June 1963; Gill 1966; Schroeder et al. 1999), but until now quantitative studies addressing its effects have not been conducted. Warm years with high growing season precipitation likely result in greater structural growth and protective cover. This may enhance nest success (Chapter 2, June 1963; Aldridge and Brigham 2002) and can elevate chick survival. Precipitation also prevents the desiccation of forbs throughout the summer months (Dunn and Braun 1986), which are important food resources for sage-grouse chicks (Kerwin 1971; Klebenow and Gray 1968; Drut et al. 1994b; Sveum et al. 1998).

Obviously it is impossible to manage climate to benefit sage-grouse populations, but it is important to recognize that weather patterns are highly variable and will indeed affect sage-grouse populations, possibly having large implications for chick survival. Thus, to ensure that populations remain viable, managers should strive to ensure high quality brood-rearing habitat exists, and that these habitats are in proximity to high quality nesting habitat, increasing the probability that hens will use these habitats and successfully fledge chicks in doing so. Providing high quality brood-rearing habitat will allow for populations to be more productive and sustain greater population numbers, buffering the negative effects of stochastic climatic events. Habitat covariates contributed to the top sage-grouse chick survival models at both the patch and area scales, and I identify habitat thresholds and provide managers with the tools necessary to develop adaptive management strategies (Aldridge et al. 2004) to enhance brood habitat and increase productivity in the Alberta sage-grouse population.

At the area scale, risk of chick failure was non-linearly related to sagebrush cover (quadratic; Table 3-19). My threshold response model suggests that moderate ranges of sagebrush cover (3-9%) result in increased risk. At the patch scale, no shrub or sagebrush variables entered into the top model, and all had low variable importance weights. This relationship, or lack of relationship with sagebrush cover, was somewhat surprising, given that my brood occurrence models showed that sage-grouse select strongly for moderate ranges of sagebrush cover. Previous research has shown that sage-grouse also show selection for sagebrush cover at brood-rearing sites prior to moving away from sagebrush uplands (Patterson 1952; Dunn and Braun 1986), selecting for forb-rich mesic habitats containing 14-40% forb cover (Peterson 1970; Schoenberg 1982; Drut et al. 1994a). Some research has shown avoidance of dense sagebrush altogether (Sveum et al. 1998). Surprisingly, hen selection for sagebrush habitats appears to compromise chick survival, and might be maladaptive, resulting in an ecological trap (Delibes et al. 2001; Donovan and Thompson 2001; Bock and Jones 2004). This relationship with sagebrush cover and chick survival needs to be explored further.

Previous work in Alberta found that a lack of forb-rich habitats likely resulted in the observed selection of sagebrush throughout the brood-rearing period (Aldridge and Brigham 2002). Although I found selection for forbs was at the patch scale, a similar pattern was not seen at the area scale. Similar to Aldridge and Brigham (2002), I found that forb availability may be limiting for sage-grouse chicks in southern Alberta, occurring at uniformly low densities across the landscape (8% cover, Table 3-1). Some of the herbaceous survival models with forbs had reasonable deviance explained (Table 3-15), yet none of my patch or area scale chick survival models containing forbs were selected as the most parsimonious top model. However, as has been suggested (but not assessed) in other studies (Peterson 1970; Schoenberg 1982; Drut et al. 1994a; Sveum et al. 1998; Aldridge and Brigham 2002) the risk of chick failure was always reduced with greater forb cover, but 95% CI overlapped 1, suggesting a very weak effect. The uniformly low availability of forbs in southern Alberta, may limit my ability to detect differences in selection, which may in turn limit my ability to detect differences in survival relative to forb availability. If forbs are important for survival but abundance is low everywhere, survival rates may be uniformly low relative to forbs. My small sample size of marked chicks (41 chicks) probably also limited my ability to detect small differences in survival. Greater than 50 marked individuals may be necessary to generate robust survival estimates (Winterstein et al. 2001).

Both the patch and area scales indicate that chick failure declined as grass cover increased. The threshold was fairly low for the larger area scale (>5% grass cover, Figure 3-4b), but patches within this area above 20-25% grass cover (Figure 3-3a) greatly reduced the risk of chick failure. However, taller grass at both scales appeared to have negative consequences for chick survival (i.e., β_{GrHgt} <1.0, Table 3-19), but threshold models illustrate habitats are not risky until grass height becomes greater than 35-40 cm (Figures 3-3b, 3-4c). Female sage-grouse are only *ca* 50 cm in length (Schroeder et al. 1999) and probably standing no more than 40 cm in height. Thus, grass cover taller than the birds may obscure their ability to detect and quickly evade predators (Wiebe and Martin 1998). These fitness cues are recognized by sage-grouse, given that hens with broods selected only moderately for tall grass cover at both scales evaluated (Table 3-8). However, despite the reduced risk for chicks in habitats with greater grass cover, sage-grouse showed strong avoidance of dense grass cover at brood rearing sites. Hens may be forced to make a trade-off between less risky habitats (tall and thick grass cover with some sagebrush cover), and having to meet dietary requirements while foraging in more open mesic habitats with less grass and structural cover that are inherently more risky. The low availability of mesic forb-rich habitats in Alberta may force hens to spend more time meeting dietary requirements, putting their chicks and possibly themselves, at greater risk of predation.

Even though my models were predictive, I did not assess the relationship between insects and habitat selection or chick survival. Insects represent an important dietary requirement of sage-grouse chicks (Kerwin 1971; Johnson and Boyce 1990; Drut et al. 1994a; Crawford et al. 2004), and recent research on other prairie grouse species has illustrated selection for insects in brood habitats (Jamison et al. 2002; Hagen et al. 2004). Selection of insects in brood rearing habitats needs to be assessed. Given the dietary limitations of chicks (Johnson and Boyce 1990), the consequences of insect abundance on chick survival should also be investigated, so that appropriate management strategies can be devised.

6. Conclusions

Sage-grouse are a relatively long-lived grouse species with low reproductive rates (Bergerud and Gratson 1988), making recruitment vital to population persistence. Thus, linking habitat requirements to juvenile survival and ultimately recruitment, are important and necessary information to appropriately identify management needs for the species (Aldridge and Brigham 2001; Crawford et al. 2004). In these analyses, I only assessed occurrence and survival using climatic and habitat covariates. However, my top models were highly predictive, explaining 44-50% of sage-grouse brood habitat selection and chick survival. This does not dismiss the need to assess brood habitat selection and chick survival at larger landscape scales, accounting for the potential effects of habitat fragmentation and human-use features such as roads, oil and gas activities and power lines.

My models represent the first attempt to assess sage-grouse chick survival as a function of habitat covariates using a shared frailty proportional hazards model to account for correlation of marked chicks within broods. I was able to identify threshold levels of grass cover and grass height necessary to ensure chick survival; providing management targets for sage-grouse brood rearing habitat in Alberta. I also show weak selection for forb-rich habitats, despite the uniformly low availability of forbs across the landscape. Although forbs were not in the top-selected proportional hazards model, chick survival was positively influenced by increased forb abundance. Further research is required into these relationships, possibly in larger populations with more variability in forb abundance and where larger sample sizes could be obtained, but the benefits of enhanced forb-rich habitats should not be dismissed, particularly for the Alberta population. Hens may be forced into an ecological trap situation (Delibes et al. 2001; Breininger and Carter 2003), spending larger amounts of time searching for poor quality forbs, which increases the risk of mortality for chicks, and possibly for hens as well.

I suggest that range management strategies be implemented to enhance cover of grass and increase the abundance of mesic habitats to enhance forb abundance. Various alternative grazing strategies and/or alternative strategies such as flooding or irrigation of rangelands needs to be used as management tools to determine the best strategy for achieving a heterogeneous mixture of these habitat conditions following adaptive management approach (Aldridge et al. 2004). Indeed, specific management will likely vary on a site by site basis and considerations for other seasonal habitat requirements (i.e., winter, nesting, lekking, and summer habitat) needs to be recognized. These management actions may take many years (>10 years in some cases) before vegetation and sage-grouse responses can be suitably assessed (Aldridge et al. 2004; Crawford et al. 2004).

Table 3-1. Explanatory habitat variables, means and standard errors (in parentheses) of values used to assess brood occurrence and chick survival for 139 brood sites and 139 paired random locations at the patch (177 m^2) and area (707 m^2) scales in southeastern Alberta from 2001-2003. When grass was absent, height values were considered zero. Models for brood occurrence were initially fit with parameters above the dashed line, validated on an independent set of data from 1998-2000, and then additional parameters only measured for 2001-2003 data were (below dashed line) were added to the top model. Chick survival data was only collected from 2001-2003, and ForbOth was not used in survival models.

Variable		177 m^2 patch scale		707 m^2 area scale	
code	Description	Brood Site	Random Site	Brood Site	Random Site
SBint	Sagebrush cover (%) estimated using line intercept	6.12 (0.52)	1.76 (0.22)	5.12 (0.42)	1.94 (0.22)
SB	Sagebrush cover (%) estimated with a 1m^2 quadrat	8.85 (0.67)	2.79 (0.34)	7.05 (0.49)	2.95 (0.30
Bush	% cover of all shrub (including sagebrush) estimated with a 1m^2 quadrat	11.65 (0.77)	4.82 (0.56)	10.02 (0.65)	5.06 (0.53)
Gr	Grass cover (%) estimated with 1m^2 quadrat	21.20 (1.15)	20.27 (1.30)	21.69 (1.14)	20.65 (0.28)
GrHgt	Mean maximum Gr Hgt (cm) within each 1m^2 quadrat	35.82 (1.20)	30.50 (1.20)	35.38 (13.40)	30.66 (1.15)
Forb	Forb cover (%) estimated with 1m^2 quadrat	8.88 (0.77)	8.07 (0.72)	8.69 (0.70)	8.01 (0.72)
ForbOth	Unpalatable (Other) forb cover (%) estimated with a 1m^2 quadrat	0.60 (0.10)	0.94 (0.12)	0.62 (0.08)	0.94 (0.11)
Robel	Visual obstruction reading (height in cm) measured at 2m from pole	10.30 (0.58)	4.95 (0.48)	9.16 (0.46)	5.20 (0.47)
Resid	Residual grass cover (%) estimated using a 1m^2 quadrat	3.61 (0.38)	3.62 (0.38)	3.63 (0.37)	3.65 (0.37)
Litter	Estimate of the cover (%) of litter build up (dead organic matter) using 1m^2 quadrat	21.20 (1.02)	16.86 (0.92)	21.22 (0.99)	17.27 (0.87)

Table 3-2. Shrub and herbaceous component models used to generate *a prior* candidate brood occurrence models based on 139 brood sites and 139 paired random nest locations in southeastern Alberta from 2001-2003 at the patch (177 m^2) and area (707 m^2) scales are shown in (a). Each of the six shrub and herbaceous component models were combined into 36 different initial candidate models (b).

a)

Shrub Component Variables	Herbaceous Component Variables
SB	Gr
SB + SB^2	Gr + GrHgt
Bush	Gr + Forb
Bush + Bush^2	Gr + GrHgt + Forb
SBint	Forb + GrHgt
SBint + SBint^2	Gr + GrHgt + Forb + ForbOth

b)

#	Structure for Sagebrush Quadrat Models	#	Structure for Bush Models	#	Structure for Sagebrush Intercept Models
1-	SB + Gr	13-	Bush + Gr	25-	SBint + Gr
2-	SB + SB^2 + Gr	14-	Bush + Bush^2 + Gr	26-	SBint + SBint^2 + Gr
3-	SB + Gr + GrHgt	15-	Bush + Gr + GrHgt	27-	SBint + Gr + GrHgt
4-	SB + SB^2 + Gr + GrHgt	16-	Bush + Bush^2 + Gr + GrHgt	28-	SBint + SBint^2 + Gr + GrHgt
5-	SB + Gr + Forb	17-	Bush + Gr + Forb	29-	SBint + Gr + Forb
6-	SB + SB^2 + Gr + Forb	18-	Bush + Bush^2 + Gr + Forb	30-	SBint + SBint^2 + Gr + Forb
7-	SB + Gr + GrHgt + Forb	19-	Bush + Gr + GrHgt + Forb	31-	SBint + Gr + GrHgt + Forb
8-	SB + SB^2 + Gr + GrHgt + Forb	20-	Bush + Bush^2 + Gr + GrHgt + Forb	32-	SBint + SBint^2 + Gr + GrHgt + Forb
9-	SB + Forb + GrHgt	21-	Bush + Forb + GrHgt	33-	SBint + Forb + GrHgt
10-	SB + SB^2 + Forb + GrHgt	22-	Bush + Bush^2 + Forb + GrHgt	34-	SBint + SBint^2 + Forb + GrHgt
11-	SB + Gr + GrHgt + Forb + ForbOth	23-	Bush + Gr + GrHgt + Forb + ForbOth	35-	SBint + Gr + GrHgt + Forb + ForbOth
12-	SB + SB^2 + Gr + GrHgt + Forb + ForbOth	24-	Bush + Bush^2 + Gr + GrHgt + Forb + ForbOth	36-	SBint + SBint^2 + Gr + GrHgt + Forb + ForbOth

Table 3-3. Model structure of additional parameters added to the top AIC$_c$-selected for brood occurrence modeling. All 139 brood sites and 139 paired random nest locations in southeastern Alberta from 2001-2003 at the patch (177 m^2) and area (707 m^2) scales were used.

Model #	Structure for 2001-2003 additional parameter models
Top #	(Top AIC$_c$-selected model for any given scale)
Top #-1	(Top model) + Robel
Top #-2	(Top model) + Resid
Top #-3	(Top model) + Litter
Top #-4	(Top model) + Robel + Resid
Top #-5	(Top model) + Robel + Litter
Top #-6	(Top model) + Resid + Litter
Top #-7	(Top model) + Robel + Resid + Litter

Table 3-4. Explanatory climate variables and models used to assess chick survival for 41 radio-marked chicks from 22 different broods in southeastern Alberta from 2001-2003. Due to small sample sizes, *a priori* climate models consisted of single parameters only. The asterisk (*) indicates that the GDD model was dropped due to violations of the proportional hazards assumption.

Model #	Variable code	Description
*1-	GDD	Cumulative growing degree days (above 5°C) since 01-March up to the given date for that specific year
2-	Sp_PPT_Cumm	Cumulative growing season (since 01 – March) precipitation for that specific year
3-	Dry_Index	An overall dryness index, calculated as the GDD (above) divided by Sp_PPT_Cumm (above)
4-	Sp_PPT_Prior	Total spring (April through June) precipitation for the spring prior to that specific year
5-	Sp-Su_PPT_Prior	Total spring and summer precipitation (April though August) of the year prior to that specific year
6-	Tot_PPT_Prior	Total precipitation for the full calendar year prior to that specific year
7-	GDD_Prior	Total growing degree days (above 5°C) from March through August for the year prior to that specific year

Table 3-5. Candidate models used to identify the best predictive shrub and herbaceous models predicting sage-grouse chick survival for 41 radio-marked chicks from 22 different broods in southeastern Alberta from 2001-2003. Due to small sample sizes, and in order to develop models with combined components, I limited herbaceous component models to two variables, and modeled each shrub component as a linear or quadratic function. I did not have a validation dataset so parameters withheld from after initial validation for brood occurrence were include in my initial candidate survival models. The asterisk (*) indicates that herbaceous model #12 was dropped due to violations of the proportional hazards assumption.

Shrub Model #	Shrub Component Variables	Herbaceous Model #	Herbaceous Component Variables
1-	SB	1-	Forb
2-	SB + SB^2	2-	Forb + Gr
3-	Bush	3-	Forb + Robel
4-	Bush + $Bush^2$	4-	Forb + Resid
5-	SBint	5-	Robel
6-	SBint + $SBint^2$	6-	Robel + GrHgt
		7-	Robel + Resid
		8-	Gr + GrHgt
		9-	Resid + GrHgt
		10-	Litter
		11-	Litter + Forb
		*12-	Litter + Robel
		13-	Litter + GrHgt

Table 3-6. AIC_c brood occurrence models and Akaike weights (w_i) for all models within a cumulative summed AIC_c weight ($\sum w_i$) of 0.90 for 139 brood locations at the patch (177 m^2) scale. All model Wald χ^2 tests were significant at $P < 0.0001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	$\sum w_i$	Model Wald χ^2	% Dev. Explained
10	SB + SB^2 + Forb + GrHgt	48.252	4	104.803	0.000	0.163	0.163	43.96	49.92
4	SB + SB^2 + Gr + GrHgt	48.313	4	104.925	0.121	0.153	0.316	43.97	49.86
3	SB + Gr + GrHgt	49.546	3	105.270	0.467	0.129	0.446	39.40	48.58
9	SB + Forb + GrHgt	49.611	3	105.400	0.597	0.121	0.567	39.41	48.51
8	SB + SB^2 + Gr + GrHgt + Forb	47.525	5	105.501	0.698	0.115	0.682	49.15	50.67
7	SB + Gr + GrHgt + Forb	48.854	4	106.007	1.204	0.089	0.771	44.33	49.29
12	SB + SB^2 + Gr + GrHgt + Forb + ForbOth	47.469	6	107.574	2.770	0.041	0.812	59.42	50.73
6	SB + SB2 + Gr + Forb	49.720	4	107.739	2.936	0.038	0.849	43.98	48.39
11	SB + Gr + GrHgt + Forb + ForbOth	48.796	5	108.043	3.240	0.032	0.882	55.28	49.35
5	SB + Gr + Forb	51.334	3	108.846	4.043	0.022	0.903	35.23	46.72

Table 3-7. AIC$_c$ brood occurrence models and Akaike weights (w_i) for all models within a cumulative 90% confidence set ($\sum w_i >$ 0.90) for 139 brood locations at the area (707 m^2) scale. All model Wald χ^2 tests were significant at $P < 0.0001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC$_c$	Δ_i AIC$_c$	w_i	$\sum w_i$	Model Wald χ^2	% Dev. Explained
28	SBint + SBint^2 + Gr + GrHgt	53.861	4	116.021	0.000	0.182	0.182	56.42	44.10
27	SBint + Gr + GrHgt	55.349	3	116.876	0.855	0.119	0.301	53.00	42.55
36	SBint + SBint^2 + Gr + GrHgt + Forb + ForbOth	52.288	6	117.212	1.192	0.100	0.401	81.46	45.73
32	SBint + SBint^2 + Gr + GrHgt + Forb	53.472	5	117.394	1.374	0.092	0.493	62.47	44.50
35	SBint + Gr + GrHgt + Forb + ForbOth	53.472	5	117.395	1.374	0.092	0.584	73.14	44.50
31	SBint + Gr + GrHgt + Forb	54.926	4	118.150	2.129	0.063	0.647	56.97	42.99
4	SB + SB^2 + Gr + GrHgt	55.068	4	118.435	2.414	0.054	0.701	46.33	42.84
34	SBint + SBint^2 + Forb + GrHgt	55.103	4	118.504	2.484	0.053	0.754	40.43	42.81
10	SB + SB^2 + Forb + GrHgt	55.270	4	118.838	2.817	0.044	0.798	44.66	42.64
33	SBint + Forb + GrHgt	56.433	3	119.044	3.023	0.040	0.839	32.95	41.43
3	SB + Gr + GrHgt	56.521	3	119.220	3.199	0.037	0.875	47.98	41.34
9	SB + Forb + GrHgt	56.527	3	119.233	3.212	0.037	0.912	39318	41.33

Table 3-8. Estimated coefficients (β_i), standard errors (shown in parentheses), and 95% confidence intervals for top AIC$_c$-selected candidate brood occurrence models in southeastern Alberta. Models were developed on 139 brood sites and 139 paired random locations collected from 2001-2003.

Variable	Patch Scale Model 10	Confidence intervals		Area Scale Model 28	Confidence intervals	
		Lower	Upper		Lower	Upper
SB	0.460 (0.083)	0.296	0.623			
SB^2	– 0.007 (0.001)	– 0.009	– 0.004			
SBint				0.757 (0.170)	0.425	1.090
SBint^2				– 0.024 (0.008)	– 0.039	– 0.009
Gr				– 0.040 (0.011)	– 0.062	– 0.017
GrHgt	0.058 (0.025)	0.010	0.107	0.115 (0.028)	0.060	0.170
Forb	0.038 (0.021)	– 0.004	0.080			

Table 3-9. Relative variable importance for brood occurrence models (2001-2003), based on the sum of the AIC_c weights for each variable across all models. (n=139 brood sites and 139 paired random locations). Sagebrush variables below the double line illustrate the strength of the measurement technique (quadrat vs. line intercept) and the importance of the quadratic relationship at each scale. Parameter Model Frequency indicates the frequency for each parameter occurring across all 36 models.

	Parameter Model Frequency	177 m^2 Patch Scale	707 m^2 Area Scale
Bush	6	0.0000	0.0000
Bush + $Bush^2$	6	0.0000	0.0003
SB	6	0.4048	0.1102
SB + SB^2	6	0.5298	0.1486
Sbint	6	0.0323	0.3138
Sbint + $SBint^2$	6	0.0330	0.4272
Grass	6	0.6963	0.8261
GrHgt	30	0.9078	0.9900
Forb	24	0.6605	0.6049
ForbOther	24	0.0780	0.2190
All sagebrush (quadrats only)	12	0.9346	0.2587
All sagebrush (intercept only)	12	0.0653	0.7410
All sagebrush (linear)	12	0.4371	0.4239
All sagebrush (quadratic)	12	0.5629	0.5758
Any with sagebrush (both measurements)	24	1.0000	0.9997

Table 3-10. Comparison of top AIC$_c$-selected brood occurrence models, metrics for overall model significance, model fit, and classification accuracy for both training (139 brood sites from 2001-2003) and testing data (113 brood sites from 1998-2000) across different scales. All model Wald χ^2 tests were significant at $P < 0.0001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model. The area under the receiver operating characteristic curves [ROC (SE)] and the percent correctly classified (PCC) based on the training dataset optimal cut off point were used to assess model classification accuracy.

Scale	Model	AIC$_c$-selected model		Model	% Dev.	Optimal	Training data		Testing data	
	#		AIC$_c$	Wald χ^2	Explained	cut-off	ROC	PCC	ROC	PCC
177 m^2 Patch scale	10	SB + SB^2 + Forb + GrHgt	104.803	43.96	49.92	0.5012	0.992 (0.015)	84.17	84.09 (0.027)	76.99
707 m^2 Area scale	28	SBint + SBint^2 + Gr + GrHgt	116.021	56.42	44.10	0.5014	0.900 (0.017)	79.14	0.8024 (0.029)	70.80

Table 3-11. Brood occurrence models and Akaike weights (w_i) for additional parameter models at the patch (177 m^2) scale for 139 brood and 139 paired random locations based on the initial 2001-2003 AIC_c-selected top model (#10). Combinations of additional parameters only measured in 2001-2003 for Robel pole, residual grass (Resid) cover, and Litter estimates comprised candidate models. All model Wald χ^2 tests were significant at $P < 0.0001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model Wald χ^2	% Dev. Explained
10	SB + SB^2 + Forb + GrHgt	48.252	4	104.505	0.000	0.364	43.96	49.92
10-1	SB + SB^2 + Forb + GrHgt + Robel	47.927	5	105.855	1.503	0.172	47.97	50.26
10-3	SB + SB^2 + Forb + GrHgt + Litter	48.089	5	106.177	1.825	0.146	47.73	50.09
10-2	SB + SB^2 + Forb + GrHgt + Resid	48.234	5	106.467	2.115	0.126	47.16	49.94
10-5	SB + SB^2 + Forb + GrHgt + Robel + Litter	47.828	6	107.657	3.490	0.064	53.17	50.36
10-4	SB + SB^2 + Forb + GrHgt + Robel + Resid	47.923	6	107.846	3.679	0.058	51.65	50.26
10-6	SB + SB^2 + Forb + GrHgt + Resid + Litter	48.083	6	108.167	4.000	0.049	51.21	50.09
10-7	SB + SB^2 + Forb + GrHgt + Robel + Resid + Litter	47.828	7	109.656	5.708	0.021	57.00	50.36

Table 3-12. Brood occurrence models and Akaike weights (w_i) for additional parameter models at the area (707 m^2) scale for 139 brood and 139 paired random locations based on the initial 2001-2003 AIC_c-selected top model (#10). Combinations of additional parameters only measured in 2001-2003 for Robel pole, residual grass (Resid) cover, and Litter estimates comprised candidate models. All model Wald χ^2 tests were significant at $P < 0.0001$. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model Wald χ^2	% Dev. Explained
28	SBint + $SBint^2$ + Gr + GrHgt	53.861	4	116.021	0.000	0.234	56.42	44.10
28-3	SBint + $SBint^2$ + Gr + GrHgt + Litter	52.897	5	116.245	0.224	0.209	57.36	45.10
28-2	SBint + $SBint^2$ + Gr + GrHgt + Resid	53.191	5	116.834	0.813	0.156	53.81	44.79
28-6	SBint + $SBint^2$ + Gr + GrHgt + Resid + Litter	52.461	6	117.558	1.537	0.109	58.61	45.55
28-1	SBint + $SBint^2$ + Gr + GrHgt + Robel	53.602	5	117.655	1.634	0.103	67.92	44.37
28-5	SBint + $SBint^2$ + Gr + GrHgt + Robel + Litter	52.734	6	118.104	2.084	0.083	69.64	45.27
28-4	SBint + $SBint^2$ + Gr + GrHgt + Robel + Resid	52.985	6	118.606	2.585	0.064	68.06	45.01
28-7	SBint + $SBint^2$ + Gr + GrHgt + Robel + Resid + Litter	52.314	7	119.483	3.463	0.041	70.90	45.70

Table 3-13. AIC_c-selected climate variable proportional hazards chick survival models and Akaike weights (w_i) for 41 chicks from 2001-2003. The Wald χ^2 is an estimate of the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (Theta). Theta is the estimate of the shared frailty variance and the *P* value for the likelihood ratio tests (LR) for the significance of the correlation is presented. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Model Structure	Theta Estimate	LR *P* value	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model Wald χ^2	Model χ^2 *P* value	% Dev. Explained
3	Dry_Index	0.314	0.283	72.46845	2	149.508	0.000	0.340	3.48	0.062	10.97
4	Sp_PPT_Prior	0.494	0.193	73.28808	2	151.148	1.639	0.150	1.45	0.229	4.68
5	Sp-Su_PPT_Prior	0.495	0.193	73.29075	2	151.153	1.645	0.150	1.44	0.230	4.66
6	Tot_PPT_Prior	0.527	0.184	73.35259	2	151.277	1.768	0.141	1.27	0.260	4.16
7	GDD_Prior	0.549	0.178	73.39109	2	151.354	1.845	0.135	1.17	0.280	3.86
2	Sp_PPT_Cumm	0.960	0.086	73.86298	2	152.297	2.789	0.084	0.00	0.995	0.00

Table 3-14. AIC_c-selected shrub variable proportional hazards chick survival models and Akaike weights (w_i) for all models at the 177 m^2 patch and 707 m^2 area scales for 41 chicks from 2001-2003 in southeastern Alberta. The Wald χ^2 indicated the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (Theta). Theta is the estimate of the shared frailty variance and the *P* value for the likelihood ratio tests (LR) for the significance of the correlation is presented. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Shrub Model Structure	Theta Estimate	LR *P* value	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model Wald χ^2	Model χ^2 *P* value	% Dev. Explained
177 m^2 Patch Scale											
1	SB	<0.001	0.437	72.022	2	148.616	0.000	0.441	6.13	0.013	14.22
5	SBint	0.052	0.483	72.854	2	150.279	1.663	0.192	3.96	0.047	8.07
2	SB + SB2	<0.001	0.500	71.974	3	151.149	2.532	0.124	5.91	0.052	14.56
3	Bush	0.777	0.158	73.363	2	151.298	2.682	0.115	1.08	0.30	4.08
4	Bush + Bush2	0.805	0.169	72.522	3	152.244	3.628	0.072	2.60	0.272	10.57
6	SBint + SBint2	<0.001	0.466	72.777	3	152.755	4.138	0.056	4.25	0.120	8.65
707 m^2 Area Scale											
6	SBint + SBint2	0.348	0.342	70.795	3	148.790	0.000	0.346	6.09	0.048	22.56
4	Bush + Bush2	0.805	0.154	71.455	3	149.924	1.134	0.196	4.34	0.114	9.42
1	SB	0.059	0.475	72.676	2	150.111	1.321	0.179	4.30	0.038	18.18
2	SB + SB2	0.109	0.455	72.034	3	151.046	2.257	0.112	4.65	0.098	5.08
5	SBint	0.326	0.351	73.237	2	151.267	2.478	0.100	2.02	0.155	14.14
3	Bush	0.871	0.125	73.759	2	152.089	3.300	0.066	0.22	0.636	0.86

Table 3-15. AIC_c-selected herbaceous variable proportional hazards chick survival models and Akaike weights (w_i) for all models at the 177 m^2 patch scale for 41 chicks from 2001-2003 in southeastern Alberta. The Wald χ^2 indicated the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (Theta). Theta is the estimate of the shared frailty variance and the *P* value for the likelihood ratio tests (LR) for the significance of the correlation is presented. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Shrub Model Structure	Theta Estimate	LR *P* value	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model Wald χ^2	Model χ^2 *P* value	% Dev. Explained
8	Gr + GrHgt	0.215	0.352	71.403	3	150.007	0.000	0.300	4.76	0.093	18.53
2	Forb + Gr	<0.001	0.500	72.106	3	151.412	1.405	0.149	4.83	0.089	13.62
1	Forb	0.798	0.110	73.562	2	151.696	1.689	0.129	0.60	0.439	2.47
5	Robel	0.923	0.091	73.831	2	152.234	2.227	0.098	0.06	0.801	0.26
10	Litter	0939	0.099	73.859	2	152.290	2.283	0.096	0.01	0.930	0.03
4	Forb + Resid	0.403	0.351	73.399	3	153.998	3.991	0.041	1.35	0.509	3.79
11	Litter + Forb	0.800	0.115	73.562	3	154.324	4.318	0.035	0.60	0.742	2.48
3	Forb + Robel	0.798	0.110	73.562	3	154.325	4.318	0.035	0.60	0.741	2.47
6	Robel + GrHgt	0.909	0.100	73.647	3	154.494	4.487	0.032	0.43	0.808	1.78
9	Resid + GrHgt	0.789	0.170	73.695	3	154.590	4.583	0.030	0.37	0.832	1.39
7	Robel + Resid	0.723	0.190	73.753	3	154.706	4.700	0.029	0.29	0.867	0.91
13	Litter + GrHgt	0.976	0.096	73.780	3	154.759	4.752	0.028	0.17	0.920	0.69

Table 3-16. AIC_c-selected herbaceous variable proportional hazards chick survival models and Akaike weights (w_i) at the 707 m^2 area scale for 41 chicks from 2001-2003. The Wald χ^2 indicated the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (Theta). Theta is the estimate of the shared frailty variance and the *P* value for the likelihood ratio tests (LR) for the significance of the correlation is presented. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Shrub Model Structure	Theta Estimate	LR *P* value	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model Wald χ^2	Model χ^2 *P* value	% Dev. Explained
8	Gr + GrHgt	0.296	0.307	72.004	3	151.208	0.000	0.202	3.70	0.157	14.35
1	Forb	0.779	0.117	73.674	2	151.920	0.713	0.142	0.40	0.529	1.56
5	Robel	0.878	0.099	73.712	2	151.995	0.787	0.136	0.30	0.583	1.25
2	Forb + Gr	0.034	0.483	72.459	3	152.119	0.911	0.128	4.02	0.134	11.04
10	Litter	0.995	0.083	73.838	2	152.248	1.040	0.120	0.05	0.822	0.21
4	Forb + Resid	0.201	0.444	73.524	3	154.248	3.040	0.044	1.61	0.448	2.79
6	Robel + GrHgt	0.843	0.115	73.544	3	154.289	3.081	0.043	0.62	0.734	2.62
3	Forb + Robel	0.779	0.118	73.619	3	154.439	3.231	0.040	0.50	0.777	2.01
11	Litter + Forb	0.805	0.114	73.645	3	154.490	3.282	0.039	0.45	0.800	1.80
7	Robel + Resid	0.745	0.204	73.692	3	154.584	3.376	0.037	0.39	0.822	1.41
13	Litter + GrHgt	1.016	0.083	73.807	3	154.814	3.606	0.033	0.11	0.944	0.47
9	Resid + GrHgt	0.802	0.188	73.809	3	154.817	3.610	0.033	0.14	0.933	0.45

Table 3-17. Overall combined candidate proportional hazards chick survival models for 41 radio-marked chicks from 22 different broods at the patch (177 m^2) and area (707 m^2) scales in southeastern Alberta from 2001-2003. The top Climate, Shrub, and Herbaceous (Herb) models were used at each scale for combination models. The top within each group was also considered as candidate models within this set. The model with the combination of 'sagebrush' + Dry_Index would not converge on a Maximun Likelihood estimate and was therefore not estimated.

	Model #	Patch Scale Combination Models		Model #	Area Scale Combination Models
1st Shrub	1-	SB	1st Shrub	1-	$\text{SBint} + \text{SBint}^2$
1st Herb	2-	Gr + GrHgt	1st Herb	2-	Gr + GrHgt
1st Climate	3-	Dry_Index	1st Climate	3-	Dry_Index
	4-	SB + Gr + GrHgt		4-	$\text{SBint} + \text{SBint}^2$ + Gr + GrHgt
	5-	Gr + GrHgt + Dry_Index		5-	Gr + GrHgt + Dry_Index
	6-	SB + Dry_Index + Gr + GrHgt		6-	$\text{SBint} + \text{SBint}^2$ + Dry_Index + Gr + GrHgt

Table 3-18. AIC_c-selected combined proportional hazards chick survival models and Akaike weights (w_i) for all models at the 177 m^2 patch and 707 m^2 area scales for 41 chicks from 2001-2003 in southeastern Alberta. The Wald χ^2 indicated the fit of the model to the data, and K indicates the number of model parameters estimated, which includes the covariates and the estimate of the random effect (Theta). Theta is the estimate of the shared frailty variance and the *P* value for the likelihood ratio tests (LR) for the significance of the correlation is presented. Percent deviance (Dev.) explained indicates the reduction in the log-likelihood from the null model.

Model #	Combined Model Structure	Theta Estimate	LR *P* value	Log-Likelihood	K	AIC_c	Δ_i AIC_c	w_i	Model Wald χ^2	Model χ^2 *P* value	% Dev. Explained
177 m^2 Patch Scale											
5	Dry_Index + Gr + GrHgt	<0.001	0.500	67.184	4	144.474	0.000	0.650	12.12	0.007	42.68
6	SB + Dry_Index + Gr + GrHgt	<0.001	0.500	67.053	5	147.440	2.966	0.148	13.11	0.011	43.30
1	SB	<0.001	0.437	72.022	2	148.616	4.142	0.082	6.13	0.013	14.22
3	Dry_Index	<0.314	0.283	72.468	2	149.508	5.034	0.052	3.48	0.062	10.97
2	Gr + GrHgt	0.215	0.352	71.403	3	150.007	5.533	0.041	4.76	0.093	18.53
4	SB + Gr + GrHgt	0.001	0.500	70.362	4	150.829	6.355	0.027	8.18	0.042	25.31
707 m^2 Area Scale											
6	SBint + $SBint^2$ + Dry_Index + Gr + GrHgt	0.314	0.283	63.377	5	140.087	0.000	0.905	16.74	0.005	58.27
1	SBint + $SBint^2$	0.348	0.342	70.795	2	146.161	6.074	0.043	6.09	0.048	22.56
5	Dry_Index + Gr + GrHgt	0.034	0.483	68.299	4	146.704	6.617	0.033	10.55	0.014	37.10
3	Dry_Index	0.779	0.117	72.468	2	149.508	9.421	0.008	3.48	0.062	10.97
4	SB + Gr + GrHgt	0.878	0.099	69.893	4	149.892	9.805	0.007	7.49	0.112	28.17
2	Gr + GrHgt	0.296	0.307	72.003	3	151.208	11.121	0.003	3.70	0.157	14.35

Table 3-19. Estimated hazard ratios (exponentiated coefficients - exp[β_i]), standard errors (shown in parentheses), and confidence intervals for top AIC$_c$-selected candidate proportional hazards chick survival combined models in south-eastern Alberta for 41 chicks from 22 different broods from 2001-2003. The top combined model at both scales had the Dry Index, the Gr + GrHgt Herbaceous component model, and a sagebrush component.

Variable	Patch scale Model # 5	Confidence intervals		Area scale Model # 6	Confidence intervals	
		Lower	Upper		Lower	Upper
Dry_Index	1.441 (0.183)	1.123	1.850	1.707 (0.268)	1.256	2.321
SBint				2.068 (0.549)	1.230	3.479
SBint^2				0.941 (0.022)	0.898	0.985
Gr	0.932 (0.026)	0.882	0.985	0.953 (0.031)	0.894	1.017
GrHgt	1.056 (0.021)	1.015	1.098	1.076 (0.027)	1.025	1.130

Table 3-20. Relative variable importance for proportional házards combination chick survival models (2001-2003), based on the sum of the AIC_c weights for each variable across all models (41 chicks). Parameter Model Freq. indicates the frequency for each parameter occurring across all 6 models.

	Patch scale		Area scale	
	Parameter Freq.	Variable Importance	Parameter Freq.	Variable Importance
SB	3	0.2566		
Sbint + $SBint^2$			3	0.9553
Gr	4	0.8656	4	0.9484
GrHgt	4	0.8656	4	0.9484
Dry_Index	3	0.8501	3	0.9464

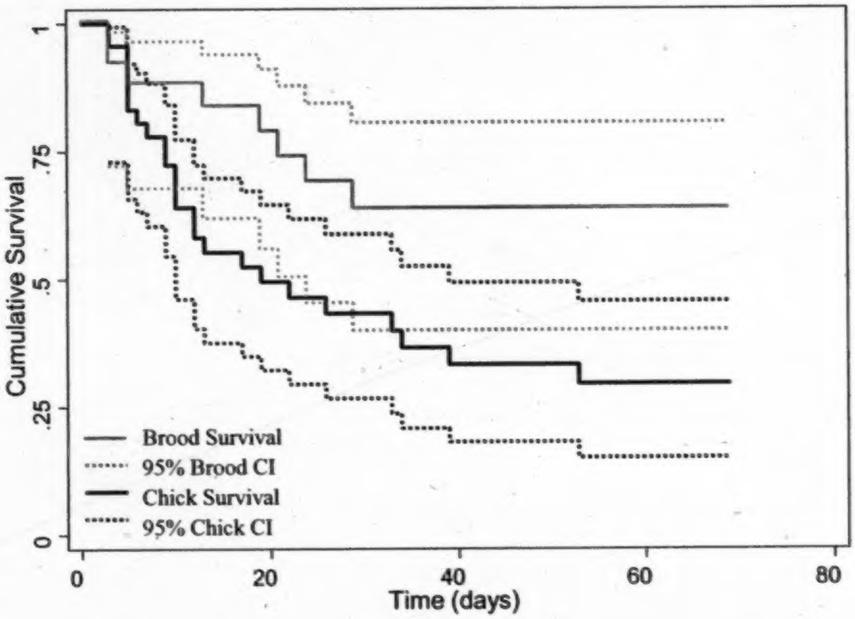

Figure 3-1. Comparison of Kaplan Meier cumulative survival curves with 95% confidence intervals for 26 different sage-grouse broods and 41 radio-marked chicks in southeastern Alberta from 2001-2003. The 41 chicks were from 22 different broods, and chick survival shown here does not take into account the correlation between chicks within a brood (maximum of two chicks marked per brood were marked).

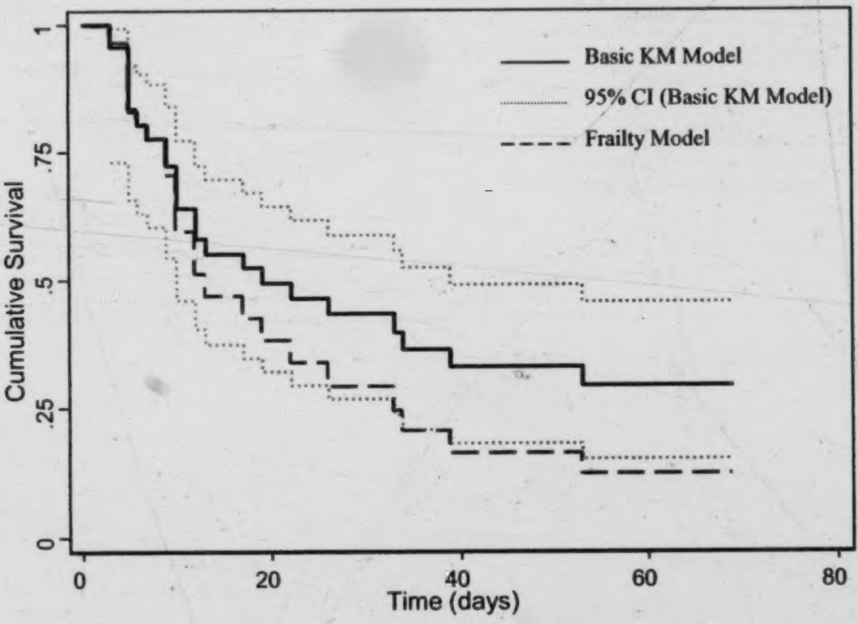

Figure 3-2. Kâplan Meier (KM) cumulative chick survival curves for 41 radio-marked sage-grouse chicks from 22 different broods in southeastern Alberta from 2001-2003. The basic KM curve (solid line) does not take into account the correlation of marked chicks within the same brood, whereas the Frailty Model (dashed line) represents that baseline Cox proportional hazard survival (i.e. no covariates) and accounts for lack of independence of siblings within the same brood. 95% confidence intervals could not be generated for the frailty model due to the conditional nature of the Cox model on covariates within the model.

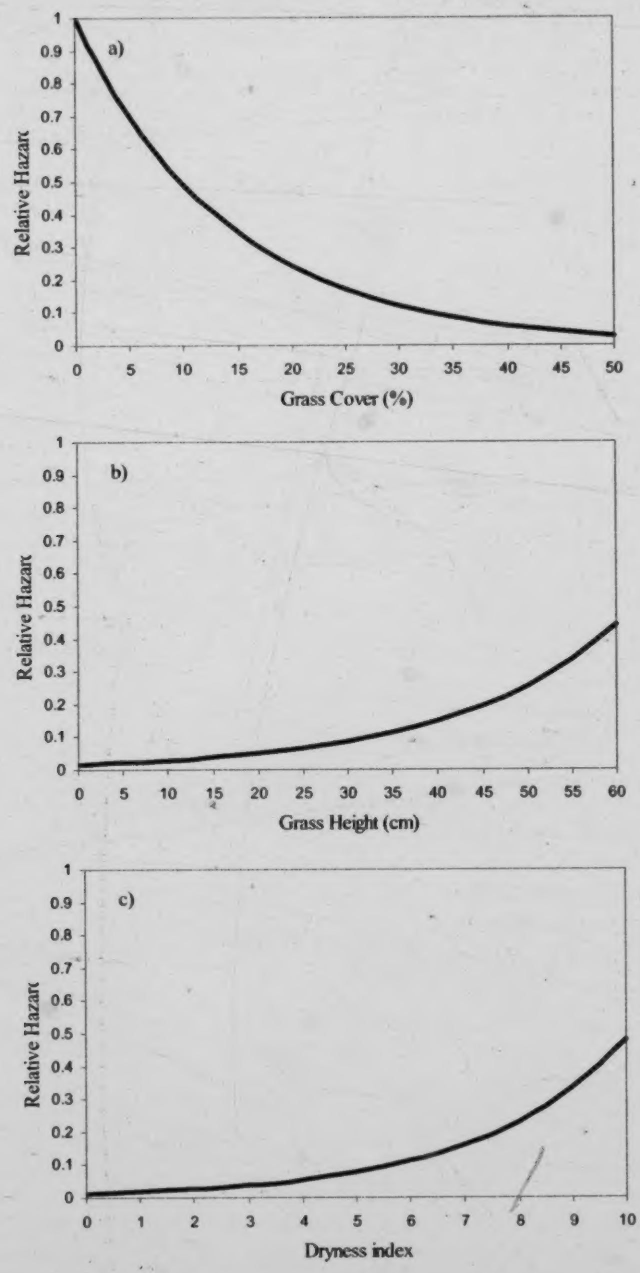

Figure 3-3. Threshold response curves for the top AIC_c-selected model (combined Model #5) at the patch scale (177 m^2) for relative risk (hazard) for sage-grouse chicks in southern Alberta. Responses are shown across the 90th percentile of availability for each parameter in the model while holding the other parameters in the model at their mean values; a) grass cover, b) grass height, and c) dryness index.

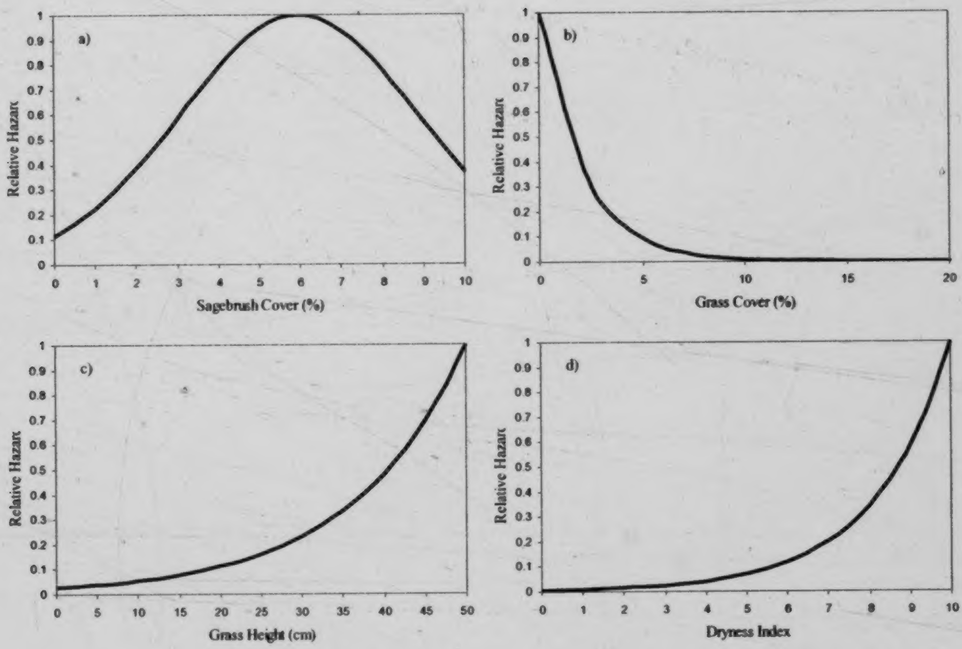

Figure 3-4. Threshold response curves for the top AIC_c-selected model (combined Model #6) at the area scale (707 m^2) for relative risk (hazard) for sage-grouse chicks in southern Alberta. Responses are shown across the 90th percentile of availability for each parameter in the model while holding the other parameters in the model at their mean values; a) sagebrush cover estimated with the line intercept method b) grass cover, c) grass height, and d) dryness index.

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Chapter Four

Linking Occurrence and Fitness: Landscape-scale Nesting and Brood-rearing Habitats for Greater Sage-Grouse in Southeastern Alberta

1. Introduction

Sagebrush-steppe ecosystems have undergone extensive changes since European settlement. Today, many of these ecosystems are considered imperilled, facing continuing fragmentation and degradation (Knick et al. 2003; Connelly et al. 2004). Increasing threats include conversion to agriculture (Connelly et al. 2004), invasion by non-native species (Knick et al. 2003; Connelly et al. 2004), energy extraction activities and developments (Braun et al. 2002; Lyon and Anderson 2003), intense grazing pressure (Beck and Mitchell 2000; Hayes and Holl 2003; Crawford et al. 2004), and climate change (Thomas et al. 2004). As a result, sagebrush-steppe dependent species have experienced drastic range contractions and population declines; one notable example being sage-grouse (*Centrocercus* spp.).

Detailed theoretical and empirical models that describe such changes are necessary to understand the underlying processes determining population persistence. While numerous local population studies focusing on fine-scale habitat correlations with various species declines have been conducted, landscape-scale habitat models (Franklin et al. 2000; Wisdom et al. 2002a; Wisdom et al. 2002b; Akcakaya et al. 2004) or range-wide analyses addressing processes and patterns of persistence have been attempted for relatively few species from only a few ecosystems (see Channell and Lomolino 2000; Mattson and Merrill 2002; Laliberte and Ripple 2004). Only a handful of these studies have integrated population dynamics with landscape-level resources (Wiegand et al. 1998; Akcakaya et al. 2004), with even fewer successfully decomposing models to critical life stages and addressing landscape-level drivers of fitness (see Breininger et al. 1998; Breininger and Carter 2003; Larson et al. 2004). This is a critical and necessary component for long-term conservation of many species of concern (Donovan and Thompson 2001) that allows biologists and managers to suitably assess population viability (Boyce et al. 1994; Boyce 2001). Ultimately, measures of habitat quality must link fitness (reproduction and survival; Van Horne 1983; Morrison 2001) to resources to accurately assess how resources affect population viability. Occurrence or abundance may not be a good indicator of fitness (Van Horne 1983; Hobbs and Hanley 1990; Tyre et al. 2001; Morrison 2001), particularly in human-dominated landscapes (Remes 2000; Bock and Jones 2004), due to the creation of ecological traps. Thus, habitat-linked population assessments should involve the identification of 1) habitats animals are likely to use (occurrence), in addition to 2) habitats where animals are likely to be successful (fitness). Habitat patches where animals are likely to occur and that also have high reproduction and/or survival measures are referred to as source habitats (Pulliam 1988; Breininger et al. 1998), whereas habitats with abundant animals but poor fitness have been referred to as 'attractive' sink habitats (Delibes et al. 2001; Breininger and Carter 2003; Larson et al. 2004) or ecological traps (Donovan and Thompson 2001; Battin 2004; Bock and Jones 2004). Failure to differentiate attractive sinks from source habitats may result in incorrect assessments of habitat importance, ultimately leading to inappropriate management strategies. However, the ability to appropriately assess habitat quality, linking habitat relationships with fitness, is limited by the difficulty in gathering suitable basic life-history information for many species (Donovan and Thompson 2001), particularly those that have low reproductive rates or are species of special concern.

The ecology of greater sage-grouse (*Centrocercus urophasianus*; hereafter 'sage-grouse') has been studied for over 100 years (Bond 1900; Burnett 1905; Simon 1940; Scott 1942), with about 20 years of extensive research on some life-history stages and various habitat-occurrence relationships (Patterson 1952; Schroeder et al. 1999; Connelly et al. 2004). Currently, sage-grouse exist in about half of their 'historic' range (Schroeder et al. 2004), with individual populations declining by 15-92% since the early 1970s (Connelly and Braun 1997; Aldridge and Brigham 2001; Connelly et al. 2004). Many populations are at risk of extirpation, reinforcing the need to appropriately assess habitat relationships for this species.

Sage-grouse population declines have been linked to low nesting success (Crawford and Lutz 1985; Aldridge and Brigham 2001; Connelly et al. 2004) and poor chick survival (Chapter 3; Aldridge and Brigham 2001; Burkepile et al. 2002). Research has shown that sage-grouse select nesting habitats with greater sagebrush cover and a more dense herbaceous understory (Aldridge and Brigham 2002), and that nest success is positively correlated with sagebrush (Chapter 2; Wallestad and Pyrah 1974; Connelly et al. 1991; Aldridge and Brigham 2002) and tall grass cover (Gregg et al. 1994; Sveum et al. 1998b; Aldridge and Brigham 2002; Watters et al. 2002; Crawford et al. 2004). Mesic habitats with abundant forbs are selected as brood-rearing habitats by female sage-grouse (Chapter 3; Klebenow and Gray 1968; Drut et al. 1994a; Sveum et al. 1998a) as the forbs and insects associated within these habitats are thought to be necessary for chick survival (Johnson and Boyce 1991; Drut et al. 1994b). Limited research on survival of individual chicks however has been conducted (Burkepile et al. 2002) and no research has assessed the links between habitats and chick survival (Chapter 3 the exception), thus far addressing only occurrence-habitat relationships (Crawford et al. 2004).

Limited research has assessed the potential landscape features driving habitat selection and fitness. For sage-grouse, other than the recently published greater sage-grouse conservation assessment (Connelly et al. 2004), which summarized sage-grouse habitats and threats range-wide, only one study to my knowledge used a habitat-based landscape approach to assess sage-grouse population persistence within the interior Columbia basin of the western United States (Wisdom et al. 2002a; Wisdom et al. 2002b),.

Within their current range, the Alberta sage-grouse population has declined 66-92% since the 1970s (Aldridge and Brigham 2001). This population is isolated from other populations and inhabits a heavily fragmented landscape, dominated by oil and gas activities (Braun et al. 2002). Recent extended drought conditions (Aldridge and Brigham 2003), and the introduction of the West Nile virus (Naugle et al. 2004) pose additional threats to the viability of this small endangered population (Aldridge and Brigham 2003), which has only 400-600 birds remaining. Low productivity limits this population (Aldridge and Brigham 2001; Aldridge and Brigham 2002; Aldridge and Brigham 2003) and the implementation of long-term habitat management initiatives may be required before increases occur (Crawford et al. 2004).

I take a 2-stage approach to identifying critical nesting and brood-rearing habitat for sage-grouse in Alberta at the landscape scale using a Geographic Information System (GIS). First, I use resource selection functions (RSFs; Manly et al. 2002) to develop spatial models predicting sage-grouse nest and brood occurrence on the landscape. Secondly, I use Cox proportional hazards survival models (Andersen and Gill 1982) to identify the most risky habitat for sage-grouse nests and for chicks. I validate the predictive capacity of these models using independent data sources. Finally, I combine these two approaches to identify attractive sage-grouse habitats that pose minimal risk of failure, referred to as primary or secondary source habitats, following Nielsen's (2005) classification. Conversely, I refer to ecological trap-type habitats that are attractive to sage-grouse but pose considerable risk, as primary or secondary sink habitats.

Considering both habitat selection and fitness allows me to identify critical sage-grouse nest and brood habitats that require protection as well as to identify attractive sink habitats that require immediate management. I discuss my findings within the context of potential reclamations or landscape improvements that could result in the transformation of non-critical habitats or attractive sink habitats into higher quality attractive source habitats. Furthermore, since 1977, management guidelines for greater sage-grouse (Braun et al. 1977; Connelly et al. 2000) have suggested that a 3.2-km buffer of habitat around known lek sites would ensure critical nesting and brood-rearing habitat is maintained. This buffer distance is based on research that indicates most females (depending of study site, between 55-100%) will nest ≤3.2 km of lek sites (see Schroeder et al. 1999). I use my empirical models to assess the effectiveness of this 3.2-km buffer at protecting critical nest and brood habitat for sage-grouse in Alberta and, simultaneously, evaluate the effectiveness of the Province of Alberta's currently recommended setback guidelines, which suggest that habitats within 1 km of known lek sites be protected and petroleum activities be limited within this 1-km radius buffer

(Scobie and Faminow 2000; Aldridge and Brigham 2003). Despite the fact that the Province of Alberta currently has no means to legally protect sage-grouse habitats, I hope that my models provide managers with the necessary tools to begin identifying critical habitat requirements for sage-grouse in Canada, as required under the federal Species at Risk Act (SARA).

2. Study area

My study area was located within the dry mixedgrass prairie of southern Alberta (49° 24' N, 110° 42' W, *ca* 900 m elevation), centred on a core sage-grouse use area (1,110 km^2) within a greater 4,000 km^2 region that they occupy (Figure 1). My study area contains 16 of the 32 historically known display sites (leks). Of these 32 lek sites, 8 are currently used by sage-grouse within the region; 5 occur within my core study area, one of which has two satellite leks within 900 m of the main lek site. This area averages 19.1°C in the summer months (July-August) and has an annual precipitation of *ca* 358 mm (Onefour Agriculture and Agri-food Canada Research Station, AAFC-AAC 2004, unpublished weather data). A large portion of this area is heavily influenced by oil and gas activities, and while little of the area within the sage-grouse range has been converted to cropland (108 km^2 within the core use area), the surrounding region is dominated by cultivated lands. Silver sagebrush (*Artemisia cana*) is the dominant shrub, and there are variety of different forb species, including pasture sage (*A. frigida*), several species of clover (*Trifolium* spp. and *Melilotus* spp.), vetch (*Astragalus* spp), and common dandelion (*Taraxacum officinale*). Needle-and-thread grass (*Stipa comata*), june grass (*Koeleria macrantha*), blue grama (*Bouteloua gracilis*), and western wheatgrass

(*Agropyron smithii*) are the dominant grass species (Coupland 1961; Aldridge and Brigham 2003).

3. Methods

3.1. Field techniques

Female sage-grouse were captured during the breeding season from 5 of 8 known active leks in southeastern Alberta from 2001 to 2004 and fitted with a 14-g necklace-style radiotransmitter (RI-2B transmitters; Holohil Systems Ltd.; Carp, ON Canada). Hens were located every second day using a 3-element Yagi antenna and an R-1000 scanning telemetry receiver (Communications Specialists, Inc. Orange, CA) so that nesting attempts and nest fate could be assessed (see Chapter 2). Nest initiation and hatch/failure were estimated as the midpoint between consecutive (every 2-days) relocations (Manolis et al. 2000) following Aldridge (Chapter 2).

From 2001-2003, if a nest was successful (i.e. ≥1 egg hatched), I captured chicks by hand as soon as possible after hatch and attached transmitters (BD-2G transmitters; Holohil Systems Ltd.; Carp, ON Canada) to 2 randomly chosen chicks from each brood following Burkepile et al. (2002; see Chapter 3 for detailed description). Hens with broods (2001-2004) and chicks (2001-2003) were relocated every 2 days during the brood-rearing period. If chick signals could not be located and the hen behaved as though she had lost her brood (i.e., flocked up), I considered the chicks to have failed on that date. All nest and brood locations were recorded in Universal Transverse Mercator Coordinates using a hand held 12 Channel Global Positioning System (Garmin 12 XL and GPS II Plus; Garmin International Inc., Olathe, KS).

3.2. GIS predictor variables

I developed a suite of variables in a geographical information system (GIS) that may be important as predictors of sage-grouse nest and brood occurrence, as well as survival of nests and chicks. Broadly, these variables were related to either habitat characteristics or human influences on the landscape (See Table 4-1 for a detailed description of each variable and its data source). First, I used a dry mixedgrass plant community guide based primarily on soil types (Adams et al. 2005) to identify 7 different greater sage-grouse ecosite range plant communities (B.W. Adams, Alberta Public Lands, Lethbridge Alberta, pers. comm.). The 8th category included all human altered landscapes (roads, well pads, urban structures, and cropland). I used dummy variable coding and indicator contrasts to assess these variables in my models. I generated variables that represented the proportion of each of habitat class within a 1-km^2 moving window across the landscape. I used a 22 July 2000 Landsat TM Satellite image (Path 39 Row 26) to generate brightness, greenness, and NDVI (Normalized Difference Vegetation Index) values using a tasselled-cap transformation of the Landsat TM bands (Crist and Cicone 1984) in the program PCI Geomatica Prime 8.2 (PCI Geomatics 2001). Brightness is a surrogate identifying exposed bare ground and poor productive soils (Crist and Cicone 1984), greenness is a surrogate for productivity that has been shown to be correlated with leaf area index (Crist and Cicone 1984; White et al. 1997), and NDVI is an alternative vegetation productivity index (Sellers 1985). I also estimated the mean and standard deviation (SD) of NDVI values (30 m X 30 m pixels) within a 1-km^2 moving window across the landscape, as I thought larger scale influences may be important.

Higher SD values should represent more heterogeneous (variable) habitat patches on the landscape.

The importance of sagebrush in providing nesting habitat (Wallestad and Pyrah 1974; Gregg et al. 1994; Aldridge and Brigham 2002; Crawford et al. 2004) has been clearly demonstrated, and it may also be selected at brood-rearing sites (Aldridge and Brigham 2002). I used a digital map of sagebrush produced by Jones et al. (2005) that was developed from air photo interpretation (Fent 1999) to estimate sagebrush cover across the landscape. Sagebrush cover is defines as the percent of each landscape polygon that was covered with sagebrush plants (Jones et al. 2005). I also estimated the mean sagebrush cover within a 1-km^2 moving window. Previous work (Chapters 2, 3) has shown that sage-grouse may not select for greater sagebrush densities linearly, selecting for intermediate cover (with a concave selection function), as very thick shrub cover can limit herbaceous understory and reduce the bird's ability to detect predators (Wiebe and Martin 1998). Thus, I assessed selection for sagebrush cover and mean cover (moving window over a 1-km^2 area) as a quadratic function. Jones et al. (2005) also categorized the density distribution of sagebrush into 12 different classes ranging from a single plant, to a continuous distribution of sagebrush. I reclassified this distribution using dummy variables to identify two measures of 'patchy' or heterogeneous sagebrush distribution (see Table 4-1). I also estimated the proportion of patchy sagebrush habitat within the 1-km^2 moving window.

Sage-grouse broods move to more mesic habitats with greater forb (Klebenow and Gray 1968; Drut et al. 1994a; Sveum et al. 1998a) and insect (Johnson and Boyce 1991; Drut et al. 1994b) abundance. Thus, I used a soil-moisture index called compound topographic index (CTI), which has been shown to be correlated with soil moisture and nutrients (Gessler et al. 1995). CTI was derived from a digital elevation model using a script in ArcGIS 8.3 (ESRI 2002) developed by Evans (2002). Similar to my lines of inference for NDVI, I also calculated measures of the mean CTI and the variability in CTI (SD) within a 1-km^2 moving widow (Table 4-1). In addition, I generated a distance to the nearest natural permanent or semi-permanent water source (Table 4-1).

Anthropogenic landscape features included the distance to roads, trails, oil well sites, crop and urban areas, as well as a density measure for each variable calculated as the linear km per km^2 for roads and trails, the number of well sites within a 1-km^2 moving window, and the proportion of the area that was either crop (cultivated lands) or urban (town, farmstead, energy infrastructure) within a 1-km^2 moving window. It has been suggested that the noise and human activity associated with road and oil wells may be avoided by (Braun et al. 2002), or have negative consequences (Lyon and Anderson 2003), for sage-grouse. Thus, I also summed the number of pixels classified as either roads or well sites, that were visible from any given cell on the landscape within 250, 500, and 1,000 m. I used a view-shed analyses tool developed by H. Beyer (University of Alberta, Edmonton, Alberta, pers. comm.) together with a digital elevation map (DEM) to generate these data. I assumed that well sites were 9 m in height, and the average vehicle driving down a road was 2 m in height, for visibility purposes. In 2001, there were ~1,890 water impediments (dams, dugouts, dam-dugout combinations, and a few irrigation berms/canals and wells) identified within the range of sage-grouse; two thirds of which are not registered or licensed impediments (McNeil and Sawyer 2003). To assess the role that these features might play in influencing habitat selection by sage-grouse, I generated a distance-to and density measure for these water impediments (Table 4-1). The final anthropogenic variables were a distance and density measure (proportion of habitat within 1-km^2 window) for human habitat (roads, oil wells, urban), and what I called any non-natural edge habitat (roads, oil wells, urban and crop).

3.3. Data Analyses

3.3.1. Model development

I began model development by conducting univariate analyses for all predictor variables (Hosmer and Lemeshow 2000), using $P < 0.25$ based on a Wald z statistic as a cut off for potential inclusion in my preliminary multivariate model. I assessed each variable for outliers and non-linearities (Hosmer and Lemeshow 1999; Hosmer and Lemeshow 2000). If two parameters were correlated ($r > |0.6|$), I retained the variable with the smallest *P*-value. I then began assessment of the full multivariate model, dropping the least significant parameter (i.e. largest *P* value), refitting the reduced model and repeating the process until all remaining parameters were significant at $\alpha = 0.05$ (Hosmer and Lemeshow 1999; Hosmer and Lemeshow 2000). I tested for multicollinearity using variance inflation factors (VIF; Menard 1995). VIF scores for individual parameters greater then 10 or mean scores for a given model considerably larger than 1 were considered problematic (Chatterjee et al. 2000), and variables were removed if this was the case. All analyses were conducted in STATA 8.2 (STATA 2004).

3.3.2. Logistic regression occurrence analyses

I evaluated 3rd-order (Johnson 1980) sage-grouse brood habitat selection using a design II approach, following individuals to identify a set of used resources, but assessing availability at the population level (Thomas and Taylor 1990; Erickson et al. 2001). I assumed that resource selection functions (RSFs) took the form:

$$\mathrm{w}(\boldsymbol{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots\ldots + \beta_p x_p) \qquad \text{(4-1)},$$

where w is the RSF for the predictor variables, x_i, and the β_i s are coefficient estimates for each predictor variable estimated using logistic regression following Manly et al. (2002:151). The RSF is equivalent to the logistic discriminant contrasting the distributions of used and available locations; if truly an RSF, the w($\boldsymbol{x}$) is a number proportional to the probability of use (Manly et al. 2002; Keating and Cherry 2004). I present coefficients for occurrence models as unstandardized linear estimates and standard errors. I generated 5,000 random locations across a 1-km buffer around a 100% minimum convex polygon surrounding all sage-grouse nest and brood locations combined (1,110 km^2 area), resulting in a density of about 5 available points per km^2. I used the same 5,000 available locations for both nest and brood occurrence analyses. The 5,000 points allowed me to accurately capture availability, but resulted in a much larger sample of available points (0) than use (1) points. I used an importance weight, which gave full weighting to use points, but available points received a weighting (down) proportional to the ratio of sampled use points to available points (STATA 2004; Users Guide). Thus, weighting effectively adjusts (inflates) the standard errors of the estimates, and allows for appropriate traditional inferences about standard errors and P-values for coefficient estimates.

3.3.3. Proportional hazards survival analyses

I used the Cox proportional hazards regression model (Cox 1972) to assess how GIS variables affect nest and chick survival. The Cox model allows for left and right censoring of data (Andersen and Gill 1982; Cleves et al. 2004) and estimates the hazard rate [$h\ (t|\mathrm{x}_i)$] for an individual *i*th subject as follows (Cleves et al. 2004):

$$h\ (t|\mathrm{x}_i) = h_0\,(t)\ \exp(\beta_{i1}\,x_{i1}+\beta_{i2}\,x_{i2}+\ldots\beta_{in}\,x_{in}) \qquad (4\text{-}2),$$

where β_i's are the regression coefficients for the x_i variables and $h_0\,(t)$ is the baseline hazard, which is not parameterized and is left unestimated. I present coefficients for all survival models as hazard ratios ($\exp[\beta_i]$) and standard errors. For chick survival models, I fit a latent random effect to account for lack of independence of chicks within broods, estimating a shared frailty Cox proportional hazards model (Therneau et al. 2003; Cleves et al. 2004; Wintrebert et al. 2005). Aldridge (Chapter 3) has previously shown that failing to account for this lack of independence will result in inappropriate survival and coefficient estimates.

I used the Breslow estimation of the continuous-time likelihood calculation (Cleves et al. 2004) to partition deaths with tied failure times. The proportional hazards model is a semi-parametric model which assumes that the effects of the covariates on survival do not change over time, except for ways in which the model is already parameterized (Cleves et al. 2004). I assessed this assumption (Winterstein et al. 2001) for my models by testing for non-zero slopes of Schoenfeld residuals and by inspecting logarithm quadrats of the estimated cumulated hazard functions (Cleves et al. 2004). Non-zero slopes (χ^2 goodness-of-fit test on the Schoenfeld residuals and non-parallel logarithm plots) indicate violations of the proportional hazards assumption Andersen and

Gill 1982; Schoenfeld 1982; Grambsch and Therneau 1994; Cleves et al. 2004). I report survival estimates as means ± standard errors.

3.3.4. Model assessment and validation

I used a χ^2 statistic (Hosmer and Lemeshow 2000) to asses the fit of all final models, except for the chick shared frailty proportional hazards model, which I used a Wald χ^2 statistic (Hosmer and Lemeshow 1999; Cleves et al. 2004). For survival models, 'relative' deviance (reduction in log-likelihood for the given model from the null model) was estimated as outlined by Hosmer and Lemeshow (1999). In addition, I estimated the cumulative daily relative risk of failure for top survival models, by summing the predicted relative hazard for each individual nest or chick and dividing it by the number of exposure days. I used these predictions to assess the predictive accuracy using receiver operator characteristic (ROC) estimates (Fielding and Bell 1997). High model accuracy results in ROC estimates above 0.9, good model accuracy between 0.7 to 0.9, and values below 0.7 indicate low model accuracy (Swets 1988; Manel et al. 2001). I used the percent correctly classified (PCC) at the optimal cut-off to estimate of the predictive capacity of the top occurrence models. PCC ≥ 80% was considered as excellent prediction and PCC ≥ 70% was considered reasonable model prediction (Nielsen et al. 2004). I also validated my nest survival model by predicting it to an independent sample of 38 nests with known fate produced by 31 different females from 1998-2000 (Aldridge and Brigham 2002, Chapter 2). I assessed fit and prediction as previously described for my model training data. I did not have an independent sample of data with which to validate the chick survival model, and limited sample sizes (41 chicks) prevented me from folding my data for cross validating (Boyce et al. 2002) purposes. Thus, for both chick and nest survival models, I took the predicted daily hazard and tested for differences in that rate of failures/deaths (nest or chick) compared to those that survived (0). If the model was predictive, chicks/nests that failed should have been exposed to greater daily hazards than those that survived. I used a one-tailed *t*-test with unequal variances to test for difference in daily relative hazard rates.

For occurrence models, it is inappropriate to assess model accuracy and predictive capacity using ROCs and PCC (Boyce et al. 2002), and deviance estimates are not true measures given use available design. Thus, I predicted the RSF in my GIS to generate relative index of occurrence scores, ranking habitats pixels into 5 bins, with bin 1 being the lowest quality bin. I then tested for a significant Spearman-rank correlation between ranked bins and frequency of used points occurring in each, after adjusting the bin for habitat availability across the landscape (Boyce et al. 2002). If the model was predictive, higher ranked bins should contain an increasing number of use points, resulting in a significant positive correlation between the bin number and area adjusted frequency of locations within that bin. Again, I validated both occurrence models using training datasets (2001 to 2004), and performed out-of-sample validation (1998 to 2000) for both models using an independent sample of 40 nest locations produced by 33 different females and 151 brood locations from 16 different broods (Aldridge and Brigham 2002, Chapters 2, 3).

3.4. Development of habitat states

I defined the 5 ranked bins for nest and brood occurrence models as 1) poor, 2) low, 3) moderate, 4) good, and 5) high occurrence, with good-to-high indices indicating that sage-grouse were likely to occur there. Similarly, I applied my survival models to my GIS landscape, ranking the predicted relative risk of failure (nest or chick) for the survival models, into 5 similar risk bins; 1) minimal, 2) low, 3) moderate, 4) high, and 5) extreme risk of failure. I used these occurrence and risk indices to identify 5 different habitat states, following the methods of Nielsen (2005). Occurrence bins ranking from poor to moderate (1-3) were classified as overall low use, and it was assumed that sage-grouse would be unlikely to occur in those habitats; although I tested this with validation data. Thus, I refer to bin 5 as primary habitat, and bin 4 as secondary habitat. In my GIS, I overlaid the respective nest or chick survival model predictions on the occurrence maps. Primary and secondary habitats falling in areas of moderate-extreme risk (bins 3-5) were classified as 'attractive' sink habitats, or primary and secondary sinks, respectively, and habitats with low risk (bins 1-2) remained as primary or secondary habitat. I graphically illustrated these conceptual habitat states in Figure 4-2. Further, I used this approach to develop maps depicting these habitat sates, summarizing the proportion of nesting and brood-rearing habitats within each habitat state. Using these models and predictive maps, I outline potential management strategies that could improve the abundance of high quality habitats for sage-grouse, and reduce the proportion of attractive sink habitats on the landscape.

4. Results

From 2001-2004 I located 113 sage-grouse nests which I used for occurrence modeling (2 nests were found from unmarked females). I used the 111 nests produced by 61 radio-marked females to assess nest survival. Nest survival to hatch (28 days) was 39.4 ± 4.84%. There was no difference in nest survival between years of my study (Log rank $\chi^2_3 = 5.50$, $P = 0.14$) and there was no difference in survival between initial (40.2 ±

5.7%, n=77) and second nesting attempts (37.5 ± 9.0%, n=34; Log rank $\chi^2_1 = 0.07$, $P = 0.79$), allowing me to combine all nests when modelling survival with GIS covariates.

From 2001-2004, I identified a total of 669 brood locations from 35 different sage-grouse broods (19.11 ± 0.60 per brood), which I used to model brood occurrence on the landscape. From 2001-2003, I radio-marked 41 chicks from 22 different broods. Chick survival to 56 days using the shared frailty proportional hazards model was 12.3% (see Figure 3-2 in Chapter 3) and there was significant correlation (at $\alpha = 0.10$) in the fate of chicks within broods ($\theta = 0.96$, $P = 0.086$) use a base model with no covariates.

4.1. Occurrence models

4.1.1. Nest occurrence

After removing all variables with $P > 0.25$, and accounting for all correlated variables ($r > |0.6|$), the preliminary multivariable nest occurrence model contained 13 variables. Stepwise removal of 7 variables based on *P*-values resulted in a final model that contained 6 parameters (Table 4-2). I tested for biologically meaningful interactions between these remaining 6 terms, and interactions with some of the 7 removed variables, but none of the interactions were significant. Thus, I used the model in Table 4-2 as my final nest occurrence model. This model had good fit (Likelihood ratio $\chi^2_6 = 53.62$, $P < 0.0001$). Based on parameters in this model, sage-grouse showed strong avoidance of badland habitats ($\beta_{pEco6} = -3.0573$), areas with high proportion of anthropogenic edge ($\beta_{pEdge} = -2.8002$), and areas with greater brightness values ($\beta_{Brit2} = -0.02115$). Conversely, sage-grouse selected nesting habitat that contained large patches (1-km^2) of moderate sagebrush cover (quadratic; $\beta_{SBmean} = 0.1025 + \beta_{SBmean2} = -0.0014$), but where the distribution of sagebrush within these patches was heterogeneous ($\beta_{pSB\_patch2} = 1.5251$; Table 4-2).

When I applied this model to the study area (Figure 4-3) and mapped and binned the landscape it into the 5 habitat bins, only 30% of the landscape was considered to have a good-to-high likelihood of sage-grouse nesting there. Both the nests (n=113) I used to build the model (2001-2004) and independent sample of 40 nest sites from 1998-2000 showed an increasing frequency (area-adjusted) of occurrence within the predicted nest index bins (Figure 4-4), justifying my classification of bins 1-3 as low use habitats. Although this relationship was not quite linear, Spearman-rank correlations on the area-adjusted frequencies and bin ranks revealed a significant positive relationship (training data: $r_s = 1.00$, $P < 0.0001$; testing data: $r_s = 1.00$, $P < 0.0001$), suggesting that the RSF for nest occurrence was approximately proportional to probability of use.

4.1.2. Brood occurrence

The preliminary multivariable brood occurrence model contained 25 variables that were not correlated and had *P*-values < 0.25. After sequentially removing the non-significant variables with the largest *P*-values, the model contained 15 significant variables. I again tested for several biologically plausible interactions, but none were significant at $\alpha = 0.05$. Thus, I used this 15-variable model as my final brood occurrence model (Table 4-3) and made inferences and prediction about this model. This model had good fit (Likelihood ratio $\chi^2_{15} = 583.32$, $P < 0.0001$). Similar to the nest occurrence model, hens with broods selected for large patches (1-km^2) of moderate sagebrush cover (quadratic; $\beta_{SBmean} = 0.10445 + \beta_{SBmean2} = -0.0010$) that contained a patchy distribution of sagebrush ($\beta_{pSB\_patch2} = 1.7924$; Table 4-3). They also showed selection for more mesic types of habitats, selecting for habitats with higher wetness values ($\beta_{Wet} = 0.0217$) and higher mean CTI scores ($\beta_{CTImean} = 0.4835$), while avoiding habitats with high brightness values ($\beta_{Brit} = -0.0076$; Table 4-3). Broods avoided habitats associated with a high density of urban developments ($\beta_{pUrban} = -64.9741$), areas close to cultivated cropland ($\beta_{Crop\_dist} = 0.1525$), and habitats composed largely of ecosite plant community type bins 4 (loamy upland sites), 5 (thin break sites), and 6 (badland sites; Table 4-3). Sage-grouse broods also tended to occur in areas with a greater density of trails ($\beta_{Tr\_dens} = 0.2336$) and were closer to water impediments than random ($\beta_{Imped\_dist} = -0.06305$; Table 4-3). Surprisingly, broods tended to be closer to well sites ($\beta_{Well\_dist} = -0.4087$), but at the same time, they avoided areas with a greater density of visible well sites within 1 km ($\beta_{vWell\_1km} = -0.2016$; Table 4-3).

I applied this 15 parameter brood occurrence model to the study area landscape (Figure 4-5), binning habitats from poor to high occurrence. Only 20% of habitat falls within the good-high habitat occurrence bins. The brood occurrence model validated well, both with the 669 brood locations I used to train the model ($r_s = 1.00$, $P < 0.0001$) and with an independent sample of 151 brood sites for 1998-2000 ($r_s = 1.00$, $P < 0.0001$). For both datasets, the area-adjusted frequency of occurrence increased with increasing brood occurrence bin rank (Figure 4-6).

4.2. Proportional hazards survival models

4.2.1. Nest survival

I retained 9 variables for the preliminary multivariate proportional hazards nest survival model after univariate analysis. After successively removing non-significant variables and testing for interactions, the final nest survival model contained 3 variables

(Table 4-4). Surprisingly, nest failure was independent of human-use features on the landscape. As was expected, nest failure was greatly reduced in habitats that contained a heterogeneous mix of sagebrush cover (β_{SBpch1} = 0.2862; Table 4-4), however, there was also a slight increase in risk as sagebrush cover in the immediate vicinity of the nest site increased ($\beta_{SBcover}$ = 1.0138; Table 4-4). In addition, as the variability in the NDVI measures increased (NDVI_sd), risk of failure decreased significantly (β_{NDVI_sd} = 10.9 x 10^{-8}; Table 4-4).

While this model had good fit (Likelihood ratio $\chi^2_3 = 12.94$, $P < 0.005$) and explained 18.05% of the variation in nest survival, when assessing it with both training and testing datasets, the model had moderate-low predictive accuracy ($ROC_{train} = 0.67$; $ROC_{test} = 0.59$) and low predictive capacity (PCC_{train} = 60.4%; PCC_{test} = 55.3%). Using the cumulative daily relative hazard, however, the nest survival model identified failed nests as being exposed to more risky habitats for the within sample dataset ($t_{102.05} = 3.52$, $P < 0.001$), but this model had difficulty differentiating failed from successful nests on the independent sample of 40 nests (22 failures; $t_{24.50} = 0.82$, $P = 0.21$). Nonetheless, when I applied this final nest survival model to my landscape, ~60% of habitat was within the moderate-extreme risk categories, in which I predict sage-grouse nests are likely to fail (Figure 4-7).

4.2.2. Chick survival

Once I removed candidate variables with $P > 0.25$, I had 7 uncorrelated variables in the preliminary multivariate chick survival model. No variables were significant (α = 0.05) when they were sequentially removed. However, the last two variables removed were significant at $\alpha = 0.10$ (β_{CTI} = 1.1883; β_{vWell_1km} = 1.5219; Table 4-5) and I choose to use these in the final model, given that my chick sample size was small (24 failures of 41 chicks). Based on these parameters, chick failure increases in habitats with a greater number of visible well sites within 1 km, and surprisingly risk was also greater in habitats with higher CTI values. Model fit was moderate (Wald $\chi^2_2 = 5.74$, $P < 0.057$), but while sample sizes were small, the model had good deviance explained (21.76%), low predictive accuracy ($ROC_{train} = 0.67$), and but good classification accuracy ($PCC_{train} =$ 70.7%). Using only these two parameters, however, my model accurately identified chicks that failed as being exposed to more risky habitats, having higher cumulative daily relative hazard rates for my within sample dataset ($t_{38.39} = 3.03$, $P = 0.002$). When I applied this model to the landscape, areas with oil and gas activities fall into the extrème risk category, but the majority of the riparian areas (with high CTI) values are also identified as risky habitats. About 60% of habitat within the study area was identified as risky for sage-grouse chicks.

4.3. Habitat States

4.3.1. Nest habitat states

By combining the nest occurrence and nest risk models, the majority (70%) of my 1,110 km^2 study area was classified as low use or non-critical nesting habitat for sage-grouse (Figure 4-9). Of the 30% of the landscape I identified with the occurrence model as having a good-high likelihood of being used as nesting habitat, over half of this habitat (19%) occurs in high risk areas, with 11.6% of habitat classified as a primary sink and 7.4% classified as secondary sink nesting habitat (Figure 4-9). Only a small portion of the landscape is primary nesting habitat (8.4%) with just 2.6% of habitat considered secondary habitat. Using a 3.2-km radius buffer around all known lek sites as a management guideline to protect sage-grouse nesting habitat, this would result in the protection of 53.9% of critical sage-grouse nesting habitat (57.8% of primary habitats and 40.0% of secondary habitats; Figure 4-10). Using a 1-km radius buffer around all lek sites following the current protective notation guidelines used by the Province of Alberta, only 9.9% of critical sage-grouse nesting habitat (11.5% of primary habitat and 4.7% of secondary habitat) would be protected (Figure 4-10).

4.3.2. Brood habitat states

My brood occurrence maps indicated that there is limited habitat available (20%) for sage-grouse brood-rearing. In addition, three quarters of that which is available is high-risk habitat, and classified as habitat sinks (15 of this 20% of the landscape is classified as a sink; Figure 4-11), leaving only 5% of the landscape as source brood-rearing habitat (primary habitat plus secondary habitat; Figure 4-11). This may explain the low chick survival rates of 12.3%. Of the currently available critical brood-rearing habitat (5% of landscape), a 3.2 km radius buffer around all known leks would result in the protection of 62% of this critical habitat (77.1% of primary habitat and 52.5% of secondary habitat; Figure 4-12). A 1-km radius buffer would protect only 9.9% of currently available critical sage-grouse brood-rearing habitat (16.0% of primary habitat and 5.7% of secondary habitat; Figure 4-12).

5. Discussion

Sage-grouse in Alberta have declined precipitously since the 1970s (Aldridge and Brigham 2003), and, similar to other populations, low recruitment appears to be the major factor driving these declines (Aldridge 2001; Crawford et al. 2004). My landscape-scale models indicate a limited supply exists of habitats selected by sage-grouse (good-to-high occurrence bins) for this population, with about 30% of the habitat likely to be used for nesting (Figure 4-3) and only 20% for brood-rearing (Figure 4-5). Of great concern is the fact that over half of those habitats identified as attractive nesting habitat (19 of 30%) are considered risky (moderate-to-extreme risk; Figures 4-7) causing an ecological trap situation (Delibes et al. 2001; Kristan 2003). Therefore, more than half of nesting habitat used by sage-grouse will not result in successful nesting attempts (Figure 4-9), even though sage-grouse still choose to occupy those habitat patches. An even greater threat to recruitment and population persistence may be the brood habitat ecological trap scenario, with three quarters of the useable brood habitat (15 out of 20% of the landscape) likely to result in chick failure (Figure 4-8). Poor quality habitats where animals have low fitness ultimately drive population dynamics (Van Horne 1983; Morrison 2001). This clearly appears to be the case for this population, which has low nest success (39%; sage-grouse range 15-86%; Schroeder et al. 1999), and extremely poor chick survival (12.3%), indicating that recruitment is unlikely to sustain this population into the near future.

Small improvements to attractive sink habitats can have disproportional changes in population persistence (Delibes et al. 2001). Thus, small changes targeted at improving portions of habitat I identify as primary and secondary nest and brood habitat sinks have the potential to greatly improve nest success and chick survival, and thus, positively influence recruitment and population viability.

5.1. Nesting habitat

Consistent with my predictions for nest occurrence and previous research at finer scales (Chapter 2), nests were more abundant in habitat patches (within a 1-km^2 area) with moderate sagebrush cover (quadratic). Selection was also strong for large patches (1-km^2) that contained a heterogeneous distribution of sagebrush cover, with continuous and sparsely distributed sagebrush habitats avoided. Moderate cover and patchy distributions likely provide suitable overstory shrub cover while allowing for lateral herbaceous cover required to conceal nests from predators (Wallestad and Pyrah 1974; Gregg et al. 1994; Wiebe and Martin 1998; Aldridge and Brigham 2002; Crawford et al. 2004). Nest abundance was lower in habitats with high brightness values, suggesting that habitats with increased bare ground were avoided. This idea is reinforced by strong avoidance of badland habitats which are characteristic of shorter annual growth cycles and steep, dry exposed soils that are less productive (B.W. Adams Alberta Public Lands, Lethbridge, Alberta, pers. comm.). My GIS based techniques were able to identify course-scale correlates for identifying this lack of herbaceous understory cover that are important for sage-grouse nesting habitat.

As I predicted, nest failure was greatly reduced in habitats that contained a heterogeneous mix of sagebrush cover (β_{SBpch1} = 0.2862), suggesting that limited sagebrush cover or continuous dense cover resulted in nest failure (Table 4-4). Conceivably, this might be why I show a slight increase in risk with increasing sagebrush cover in the immediate vicinity of the nest site (linear increase; $\beta_{SBcover}$ = 1.0138; Table 4-4). Risk also was significantly reduced for increasing NDVI_sd measures. The extremely small nature of the measure is somewhat deceptive, because NDVI index values were small, ranging from 0.012 to 0.099. Taking the natural logarithm of the unexponentiated β coefficient (β_{NDVI_sd} = – 18.33) times an increase in the NDVI_sd index values of 0.01 (about 10% of range for nest sites) indicates that nest survival would increase by about 17% (exp[– 18.33 * 0.01] = 0.833). Thus, the idea that more diverse heterogeneous habitats reduced risk also was supported by the small hazard ratio for the NDVI variability measure (Table 4-4).

Surprisingly, the proportion of any single human-use feature within a 1-km^2 area did not enter into my final nest occurrence model, but when roads, well sites, urban habitats, and cropland were combined into one parameter (pEdge), sage-grouse strongly avoided nesting in these edge-dominated landscapes. Hens may be responding to increased predator densities associated with edge-type habitats (Andren and Angelstam 1988; Herkert et al. 2003) and agricultural landscapes (Andren 1992; Kurki et al. 2000), avoiding these more risky edge habitats that have been shown to negatively impact prairie grouse populations (Fuhlendorf et al. 2002; Manzer 2004). However, similar to many other studies assessing fragmentation effects on productivity (Pasitschniak-Arts and Messier 1995; Svobodova et al. 2004) I found no effect of edge, or other human features on sage-grouse nest success (Table 4-4). Pitman (2003) found that nest placement for lesser prairie-chickens (*Tympanuchus pallidicinctus*) in Kansas were further from paved roads than at random. In the same area, Hagen (2003) showed that proximity to human structures greatly reduced habitat suitability, while roads had no obvious effect. However, neither of these studies addressed fitness relative to anthropogenic features. The mean proportion of edge habitat within a 1-km^2 window around nests sites was 2.9 ± 0.7%, compared to an average of 10.1 ± 0.3% edge habitat across the landscape. Thus, females' strong avoidance of edge habitats ($\beta_{pEdge} = -2.80$) for nesting likely prevented my ability to detect survival differences relative to these features.

Ecological traps tend to be more prevalent in human dominated landscapes (Remes 2000; Bock and Jones 2004), with birds failing to recognize these risks in landscapes in which they did not evolve, such as human-fragmented habitats. Sage-grouse, however, may recognize some of these habitats as risky, avoiding potential ecological traps created in human-dominated habitat patches; at least when selecting nesting habitat. This does not mean that human features have no ill effects on nesting sage-grouse. Avoidance of these features removes that habitat patch from use by sage-grouse, and effectively removes habitat within a 564-m radius (1-km^2 area) of those patches as potential nesting habitat (functional habitat loss). This zonal-habitat influence may be greater, but I did not test the effect of edge habitat density in windows greater than a 1-km^2 area. Even though sage-grouse might recognize and avoid these anthropogenic threats, half of all high use nesting (good-to-high rank) habitats are still considered attractive sinks (Figure 4-9); ecological traps driven by habitat features. I suggest that my maps be used to identify risky nesting habitats, and managers should focus efforts at improving nest success by establishing a heterogeneous mix of sagebrush patches in these areas. Management of local range conditions (Crawford et al. 2004) aimed at enhancing grass and forb understory that improves visual obstruction cover in these risky nesting areas (Chapter 2) will likely be required to convert into sinks into source-type habitats. Range conditions should be assessed locally (see Chapter 2) and grazing could be a tool used to adaptively manage and enhance these habitats (Aldridge et al. 2004).

5.2. Brood-rearing habitat

As predicted, and has been shown at more local scales (Aldridge and Brigham 2002; Chapter 3), sage-grouse also selected for moderate ranges of sagebrush cover at sites used for brood-rearing. Brood occurrence also was greater in more heterogeneous sagebrush stands, because these patchy habitats provide cover to reduce predator efficiency (Wiebe and Martin 1998) but still afford necessary forb resources. Boyce (1981) demonstrated that sage-grouse were more abundant in patchy habitats containing a mix of mesic forb-rich foraging areas interspersed within suitable densities of sagebrush escape cover.

Brooding hens showed strong avoidance of human-dominated landscapes, avoiding areas closer to cultivated cropland and areas that contained a greater proportion of urban developments. With the exception of feeding on some cereal crop such as alfalfa (Patterson 1952), sage-grouse do not regularly use agricultural dominated landscapes. Cultivation directly removes habitats from the perspective of sage-grouse, and has been correlated with sage-grouse population declines in Idaho (Leonard et al. 2000).

Conversely, sage-grouse may only partially recognize some ecological cues related to anthropogenic features that make habitat risky to chicks. Although hens with broods tended to be closer to oil wells then at random, they avoided habitats with a greater density of visible oil wells. This relationship may partially be due to the static nature of my GIS landscape, for which well sites were fixed at the known distribution on the landscape in 2002. In some cases, sage-grouse broods occurred close to well sites, but not often in areas with high well densities (Figure 4-5). However, my chick survival model predicts a 1.5 times increase in risk for each additional oil well that is visible within 1 km of brood locations (see Figure 4-7). As a result, a significant portion of primary and secondary brood habitat is classified as attractive sink habitats (see Figure 4-11). I am not suggesting that the well sites are killing sage-grouse, but birds have been run over by vehicles travelling on the associated roads (C.L. Aldridge, unpublished data), and raptorial predators, such as golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo regalis*), red-tailed hawks (*Buteo jamaicensis*), great horned owls (*Bubo virginianus*), and others, are often observed perching on the power lines associated with these well sites, conceivably exposing sage-grouse chicks to an increased risk of predation. Regardless of the mechanism, chicks have a low probability of survival, which is further reduced when energy extraction activities dominate the landscape.

Similar to nest occurrence, sage-grouse broods avoided the less productive and more exposed badland range plant community habitats (pEco6). Broods also showed strong avoidance of the thin-break range sites (pEco5), and the loamy upland sites (pEco4; Table 4-3). The thin-break sites are similar to badland habitats, but contain greater sagebrush cover, and the loamy upland sites are more productive range sites, but are dominated by various graminoid species, resulting in a lack of shrubs and forbs (B.W. Adams, Alberta Public Lands, Lethbridge, Alberta, pers. comm.). Thus, while these 2 sites might provide added cover from either sagebrush or dense grass cover, they lack the forb component required by sage-grouse broods.

Sage-grouse broods selected for more mesic habitats. This was reflected in brood occurrence being associated with lower brightness values, and higher mean CTI and wetness values (Table 4-3). These habitats are likely required for birds to meet dietary requirements, as forb (Klebenow and Gray 1968; Drut et al. 1994a; Sveum et al. 1998a) and insect abundance is enhanced in these habitats (Johnson and Boyce 1991; Drut et al. 1994b). Hens also chose to be closer to water impediments on the landscape. The effect of altered water hydrology on the vegetation productivity, composition, and distribution within this xeric ecosystem needs to be investigated. Removing some of these impediments on the landscape may effectively return water to the system, and recharge some of these former mesic sites, rather than retaining water behind a dam or in a dugout. This could be tested as an adaptive management experiment (Chapter 5; Aldridge et al. 2004), which would provide useful insights into the hydrology of the dry mixedgrass system and vegetation responses, and may result in improved abundance and quality of mesic brood-rearing habitats for sage-grouse.

Although mesic habitats were selected, higher CTI values resulted in increased risk of chick failure. Excluding the high risk values associated with greater well-site densities (Figure 4-8), the majority of other high CTI risky habitats occurred in riparian habitats along creeks and streams. While these habitats are not frequently used by sage-grouse broods (see Figure 4-5), there may be increased risk with these shrubby riparian corridors, which often contain a greater concentration of predators (Wilcove 1985). In Chapter 3, I showed that more mesic forb-rich habitats preferred by sage-grouse broods tend occur in more risky open habitats. I hypothesized that sage-grouse may be making trade-offs between habitats that provide protective escape cover and risky open mesic habitats that provide necessary forage resources. This also could be an additional explanation for the increased risk of chick failure associated with high CTI values. Recent droughts could have made these habitats even more risky for sage-grouse chicks, particularly if livestock grazing intensities were not subsequently reduced. These relationships are poorly understood (Crawford et al. 2004) and need to be investigated within a long-term adaptive management framework (Aldridge et al. 2004; see Chapter 5).

5.3. Leks as focal points for habitat protection

For all prairie grouse the lek is thought of as the focal point for year-round activities. Much research has focused on maintaining required habitats surrounding leks and attempting to identify links between habitat alterations and lek dynamics (Merrill et al. 1999; Niemuth 2000; Woodward et al. 2001; Fuhlendorf et al. 2002; Niemuth and Boyce 2004). However, my approach of modeling and mapping high-quality nesting and brood rearing habitats suggests that such a heavy focus on habitat protection around lek sites may not be suitable to ensure the viability of sage-grouse populations. Using the recommended 3.2-km radius buffer around known (active and inactive) Alberta lek sites as a guide (Braun et al. 1977; Connelly et al. 2000), only 54% of critical nesting habitat (primary and secondary habitat; Figure 4-10) and 62% of critical brood habitat (primary and secondary habitat; Figure 4-12) would be protected. Given the limited availability of high-quality habitats within this landscape, protecting only 60% of source habitats may not be enough to ensure that this population remains viable.

Perhaps even more alarming, is the fact that the 1-km radius buffer around lek sites used by the Province of Alberta (Scobie and Faminow 2000) will protect less than 10% each of critical nesting and brood-rearing habitat. These guidelines need to be revised to prevent the quick demise of sage-grouse in Alberta. Even if one used the mean nest-to-closest active lek distance for this population (4.9 ± 0.28 km, n =153, C.L.

Aldridge unpublished data) as a lek-protection buffer, only about 75% of critical nesting and brood-rearing habitat would be protected. I suggest a more insightful management approach, using these models and maps to identify and protect important primary and secondary nesting and brood-rearing habitats throughout the landscape. Given that sage-grouse show high fidelity to nesting and brood-rearing areas (C.L. Aldridge, unpublished data; Fischer et al. 1993; Schroeder and Robb 2003) this approach may be particularly effective, allowing for direct mitigation within frequently used 'attractive' sink habitats, while limiting the negative effects of rampant energy development in the area. However, careful attention still needs to be given to managing other seasonal habitat requirements, such as lekking, summer, and winter habitat, and maintain connectivity between these habitats.

6. Conclusions

I show that a large proportion of habitats used by sage-grouse for nesting and brood-rearing pose high risks. Sage-grouse appear to recognize and avoid some of these risky habitats, but still select for others, apparently resulting in ecological traps. Given the low nest (39%) and chick (12%) survival, it may not be a question of whether or not sage-grouse are capable of recognizing the risks, as they do avoid (low occurrence) some of these more risky habitats. Instead, it may simply be that the majority of habitats they require present major risks to nests or chicks, either due to anthropogenic causes (i.e. edge habitat, well-site density) or due to limited 'natural' habitat resources. Habitat quality may have been reduced by altered grazing regimes (Beck and Mitchell 2000; Crawford et al. 2004), altered fire frequencies (Adams et al. 2004), increases in drought events (Adams et al. 2004), or global change (Thomas et al. 2004). The causes may be diverse, but high-quality habitats are limiting and the conversion of sink habitats into sources will enhance the viability of sage-grouse in Alberta.

I propose these models as the framework for evaluating management alternatives aimed at increasing productivity through addressing habitat-quality issues with a habitat-based population viability analysis approach (Boyce et al. 1994; Boyce and McDonald 1999). My models should be used to identify priority areas that need to be protected (primary and secondary habitats). In these habitats, further developments should be prevented to avoid turning these source habitats into sinks. Where developments currently exist, such that habitat is an attractive sink for sage-grouse, improvements are necessary to reduce the risk. Edge-type habitats could be removed, including the removal or decommissioning of roads, possibly through the sharing of road access between oil companies. Well sites may need to be removed and well pads reclaimed, to reduce threats to sage-grouse chicks. Power lines have negative consequences for prairie grouse (Hagen 2003; I did not directly assess this in my study), and power poles may need to be capped to reduce the number of accessible perch sites for raptors that prey on sage-grouse, or buried, which will also reduce fatal sage-grouse-power line collisions (Borell 1939).

On a local scale, management will need to focus on structural cover provided by sagebrush, grass and forbs, and increasing the abundance of mesic habitats that provide important food resources (forbs and insects). Indeed, management prescriptions for these priority areas will have to occur on a site-by-site basis, after appropriate assessments have been conducted. These models and maps provide managers with the tools to assess and prioritize management needs, as well as to evaluate habitat management strategies in an adaptive management framework (Chapter 5; Aldridge et al. 2004).

Table 4-1. Explanatory GIS raster variables used for 3rd order sage-grouse occurrence and survival models for sage-grouse nests and broods. All variables were first tested univariately in occurrence (logistic regression) and survival (proportional hazards) models. Candidate variables with $P < 0.25$ were removed, and correlated variables with higher *P*-values were removed. Data type refers to continuous (cont.) or categorical (cat.) variables. All distance measures are in km.

Variable	Data type	Description
Brit	30m cont.	Brightness generated from a Landsat 7 TM satellite image
Green	30m cont.	Greenness generated from a Landsat 7 TM satellite image
Wet	30m cont.	Wetness generated from a Landsat 7 TM satellite image
NDVI	30m cont.	Natural Difference Vegetation Index calculated from a TM satellite image
NDVI_avg	30m cont.	Mean NDVI value within a 1-km^2 moving window
NDVI_sd	30m cont.	Standard deviation of NDVI within a 1-km^2 window
CTI	30m cont.	Compound Topographic Index (high values = increased moisture)
CTI_mean	30m cont.	Mean CTI values within a 1-km^2 moving window
CTI_sd	30m cont.	Standard deviation of CTI values within a 1-km^2 moving window
Well_dist	10m cont.	Distance to nearest standing energy well site
Well_dens	10m cont.	Count of energy well sites within a 1-km^2 moving window
vWell_1km	30m cont.	Count of the number of 30 m pixels within a 1km radius that are well sites
vWell_500m	30m cont.	Count of the number of 30 m pixels within a 500 m radius that are well sites
vWell_250m	30m cont.	Count of the number of 30 m pixels within a 250 m radius that are well sites
Rd_dst	10m cont.	Distance to nearest road (any paved or gravel road)
Rd_dens	10m cont.	Liner km per km^2 of roads
vRd_1km	30m cont.	Count of the number of 30 m pixels within a 1km radius that are road
vRd_500m	30m cont.	Count of the number of 30 m pixels within a 500 m radius that are road
vRd_250m	30m cont.	Count of the number of 30 m pixels within a 250 m radius that are road
Tr_dst	10m cont.	Distance to nearest trail (non-paved or gravelled truck trail)
Tr_dens	10m cont.	Liner km per km^2 of trails
Imped_dst	10m cont.	Distance to nearest water impediment (dam, dugout, dam-dugout combination)
Imped_dens	10m cont.	Count of the number of water impediments within a 1-km^2 moving window
Water_dst	10m cont.	Distance to the nearest natural permanent or semi-permanent water body
SB	10m cont.	% Sagebrush cover as identified from air photo interpretation
SB^2	10m cont.	Squared term for SB
SBmean	10m cont.	Mean % sagebrush cover within a 1-km^2 moving window
$SBmean^2$	10m cont.	Squared term for SBmean
SB_pch1	10m cont.	Patchy sagebrush distribution 1- (codes 7, 8, and 9 of Jones et al. 2005)
pSB_pch1	10m cont.	Proportion of habitat within a 1-km^2 moving window that is SB_pch1
SB_pch2	10m cont.	Patchy sagebrush distribution 2-(codes 7, 8, 9 and 11 of Jones et al. 2005)
pSB_pch2	10m cont.	Proportion of habitat within a 1-km^2 moving window that is SB_pch2

Table 4-1 (continued)

Variable	Type	Description
Crop_dst	10m cont.	Distance to nearest cultivated lands
pCrop	10m cont.	Proportion of habitat within a 1-km^2 moving window that is cultivated
pUrban	10m cont.	Proportion of habitat within a 1-km^2 moving window that is urban (town, ranch, energy compressor station etc.)
Urban_dst	10m cont.	Distance to nearest urban developments
Eco1	10m cat.	Loamy range site with well drained soils, low sagebrush cover
Eco2	10m cat.	Saline lowlands, swales and depression, spares low sagebrush
Eco3	10m cat.	Blowout and overflow sites, solonetzic soils; plant community varies, but higher density of sagebrush
Eco4	10m cat.	Loamy upland sites with medium texture soils, fescue & wheatgrasses
Eco5	10m cat.	Thin break range sites, soils vary, characterized by greater shrub cover
Eco6	10m cat.	Badlands type habitats with juniper and needle-and-thread-blue grama
Eco7	10m cat.	Broad, wetland and shrubby (willow, rose, snowberry) riparian habitats
Eco8	10m cat.	All altered habitats (urban, crop, wells and roads) see also Hum and Edge below
pEco1	10m cont.	Proportion of habitat within a 1-km^2 moving window that is Eco1
pEco2	10m cont.	Proportion of habitat within a 1-km^2 moving window that is Eco2
pEco3	10m cont.	Proportion of habitat within a 1-km^2 moving window that is Eco3
pEco4	10m cont.	Proportion of habitat within a 1-km^2 moving window that is Eco4
pEco5	10m cont.	Proportion of habitat within a 1-km^2 moving window that is Eco5
pEco6	10m cont.	Proportion of habitat within a 1-km^2 moving window that is Eco6
pEco7	10m cont.	Proportion of habitat within a 1-km^2 moving window that is Eco7
Hum_dst	10m cont.	Distance to any human habitat (roads, wells, urban)
pHum	10m cont.	Proportion of habitat within a 1-km^2 moving window that is human habitats
Edge	10m cont.	Distance to habitat that creates non-natural edge (human above + crop)
pEdge	10m cont.	Proportion of habitat within 1-km^2 moving window that is edge

Notes:

-TM derived variables were based on a 22 July 2000 Landsat 7 image (Path 39 Row 26)
-Digital elevation model derived from 1:50,000 National Topographic Database Contour Lines
-Sagebrush, crop, urban, and water base features Jones et al. (2005)
-Sagebrush cover is the percent of area within each polygon covered by sagebrush (Jones et al. 2005)
-Linear Features based on a 2001 landscape from Alberta Provincial Base features (1:20,000)
-Well locations provided by Alberta Energy for the study area as of August, 2002
-Water impediments were mapped based on (McNeil and Sawyer 2003)
-Eco1to Eco7 are dry mixedgrasss rangeland ecosite plant community bins after (Adams et al. 2005)

Table 4-2. Estimated coefficients (βi) and standard errors (S.E.) for the final nest occurrence model for 113 sage-grouse nests in southeastern Alberta from 2001-2004. 5,000 random points were used to characterise habitat availability and these points were weighted using importance weights such that the available sample was effectively 113 points. P values indicated the significance of the coefficients using a Wald z statistic.

Variable name	β_i	S.E.	*P*
Brit	– 0.0215	0.0082	0.009
SBmean	0.1025	0.0401	0.011
SBmean^2	– 0.0014	0.0007	0.047
pSB_pch2	1.5251	0.7602	0.045
pEco6	– 3.0573	0.9654	0.002
pEdge	– 2.8002	1.3531	0.038

Table 4-3. Estimated coefficients (β_i) and standard errors (S.E.) for the final brood occurrence model for 669 sage-grouse brood locations in southeastern Alberta from 2001-2004. 5,000 random points were used to characterise habitat availability and these points were weighted using importance weights such that available sample was effectively 669 points. *P* values indicated the significance of the coefficients using a Wald *z* statistic.

Variable name	β_i	S.E.	*P*
Brit	– 0.0076	0.0032	0.018
Wet	0.0217	0.0088	0.013
CTI_mean	0.4835	0.0872	< 0.001
Well_dist	– 0.4087	0.0446	< 0.001
vWell_Ikm	– 0.2016	0.0591	0.001
Tr_dens	0.2336	0.0887	0.008
Imped_dist	– 0.6305	0.2134	0.003
SBmean	0.1044	0.0175	< 0.001
SBmean^2	– 0.0010	0.0003	< 0.001
pSB_pch2	1.7924	0.3703	< 0.001
Crop_dist	0.1525	0.0339	< 0.001
pUrban	– 64.9741	18.2819	< 0.001
pEco4	– 1.2791	0.3625	< 0.001
pEco5	– 2.1208	0.3368	< 0.001
pEco6	– 1.8744	0.4931	< 0.001

Table 4-4. Estimated hazard ratios (exponentiated coefficients - exp[β_i]) and standard errors (S.E.) for the final proportional hazards nest survival model using 111 sage-grouse nest sites in southeastern Alberta from 2001-2004. *P* values indicated the significance of the coefficients using a Wald *z* statistic.

Variable name	β_i	S.E.	*P*
NDVI_sd	$10.9 * 10^{-8}$	9.44	0.034
SB	1.0138	0.0052	0.007
pSBpch1	0.2862	0.1784	0.045

Table 4-5. Estimated hazard ratios (exponentiated coefficients - exp[β_i]) and standard errors (S.E.) for the shared frailty final proportional hazards chick survival model using 41 sage-grouse chicks from 22 different broods in southeastern Alberta from 2001-2003. *P* values indicated the significance of the coefficients using a Wald *z* statistic. The shared Frailty variance estimate was $\theta = 1.246$, $P = 0.047$.

Variable name	β_i	S.E.	*P*
CTI	1.1883	0.1145	0.073
vWell_1km	1.5219	0.3437	0.063

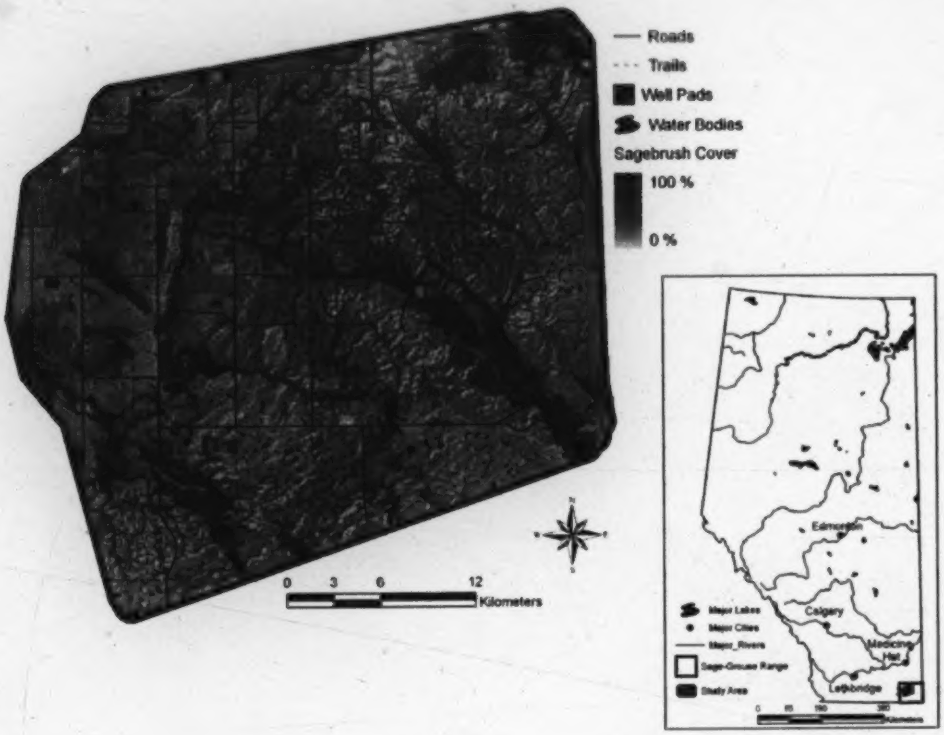
Roads
Trails
Well Pads
Water Bodies
Sagebrush Cover
100 %
0 %
0
3
6
12
Kilometers
Edmonton
Calgary
Medicine Hat
Lethbridge
Major Lakes
Major Cities
Major_Rivers
Sage-Grouse Range
Study Area

Figure 4-1. Alberta greater sage-grouse study area showing sagebrush density with roads, trails, well pads, and major water bodies. Inset map shows the study area and current range of sage-grouse within Alberta, with major rivers, water bodies, and cities for reference.

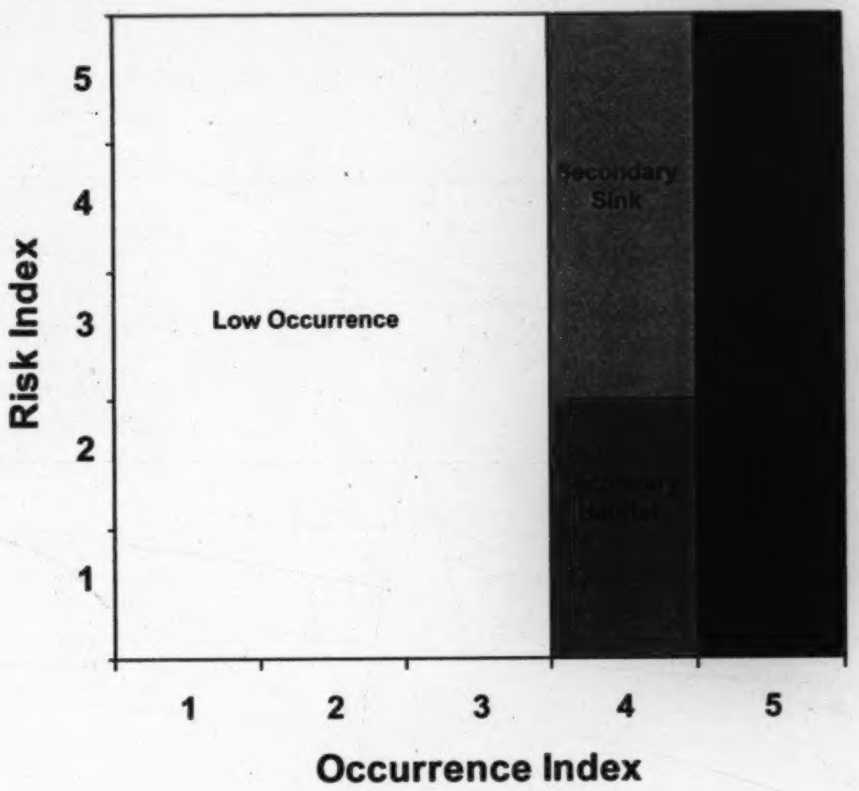

Figure 4-2. A graphic representation of nesting and brood-rearing habitat states for sage-grouse in southeastern Alberta. States include non-critical (low occurrence) habitat, Primary Habitat (high occurrence and low- moderate risk), Secondary Habitat (good occurrence and low-moderate risk), Primary Sink (high occurrence and moderate-extreme risk), and Secondary Sink (high occurrence and moderate-extreme risk). Adapted from Nielsen (2005).

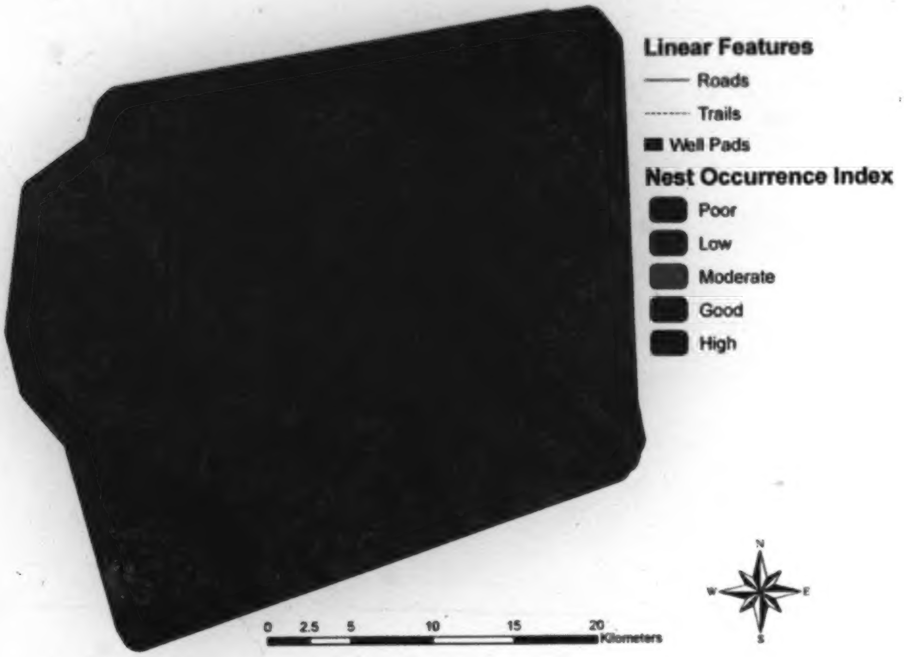
Linear Features
Roads
Trails
Well Pads
Nest Occurrence Index
Poor
Low
Moderate
Good
High
0 2.5 5 10 15 20 Kilometers
N
W
E
S

Figure 4-3. Relative index of sage-grouse nest occurrence in southeastern Alberta, as determined by a logistic regression nest occurrence model. Good and high index values indicate that sage-grouse are likely to nest in these habitats.

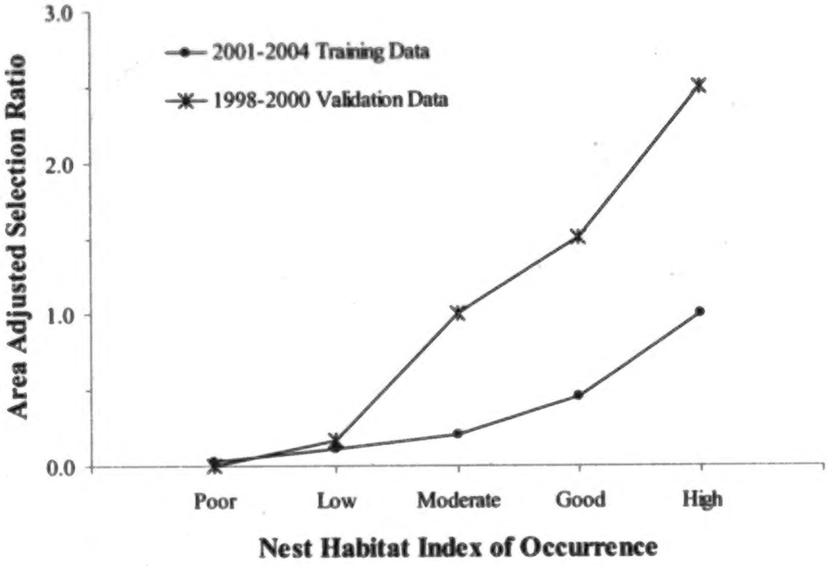

Figure 4-4. Area-adjusted frequency of sage-grouse nest sites in southeastern Alberta falling within nest habitat index of occurrence bins ranked as poor, low, moderate, good, and high. Training data consists of 113 within sample nest sites from 2001-2004 and the Validation sample consists 40 out-of-sample nest sites from 1998-2000.

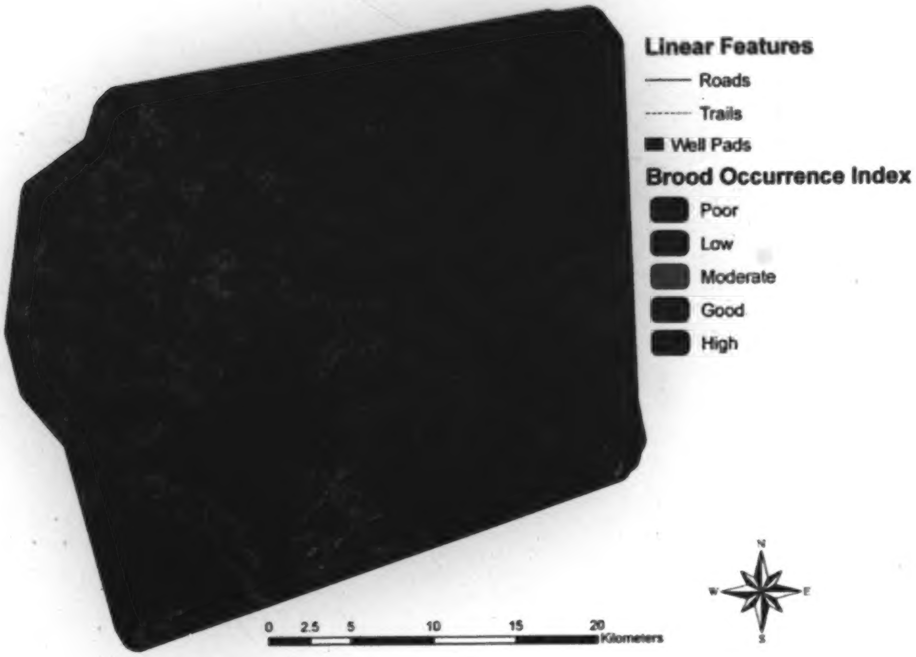
Linear Features
Roads
Trails
Well Pads
Brood Occurrence Index
Poor
Low
Moderate
Good
High
0 2.5 5 10 15 20
Kilometers
N
W
E
S

Figure 4-5 Relative index of sage-grouse brood occurrence in southeastern Alberta, as determined by a logistic regression brood occurrence model. Good and high index values indicate that sage-grouse are likely to raise their broods in these habitats.

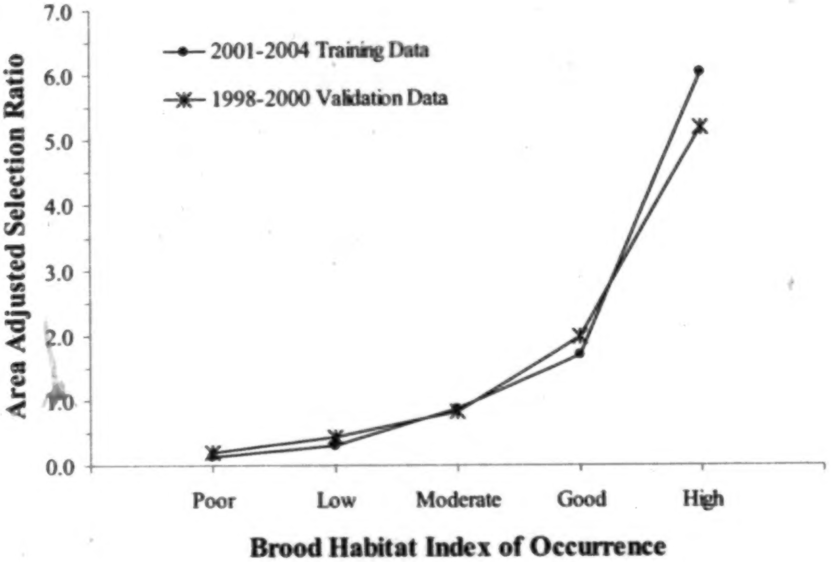

Figure 4-6. Area-adjusted frequency of sage-grouse brood sites from southeastern Alberta falling within brood habitat index of occurrence bins ranked as poor, low, moderate, good, and high. Training data consists of 669 within sample brood sites from 2001-2004 and the validation sample consists 151 out-of-sample brood sites from 1998-2000.

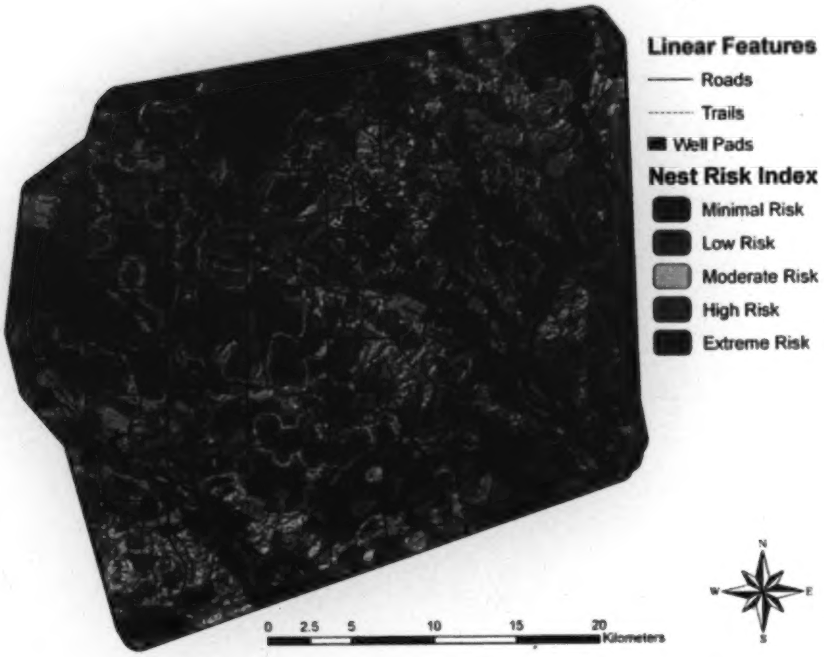
Linear Features
Roads
Trails
Well Pads
Nest Risk Index
Minimal Risk
Low Risk
Moderate Risk
High Risk
Extreme Risk
0
2.5
5
10
15
20
Kilometers
N
W
E
S

Figure 4-7. Relative index risk of sage-grouse nest failure in southeastern Alberta, as determined by Cox proportional hazards modelling of nest survival. High and extreme risk values indicated a nest is likely to fail if it occurs in these habitats.

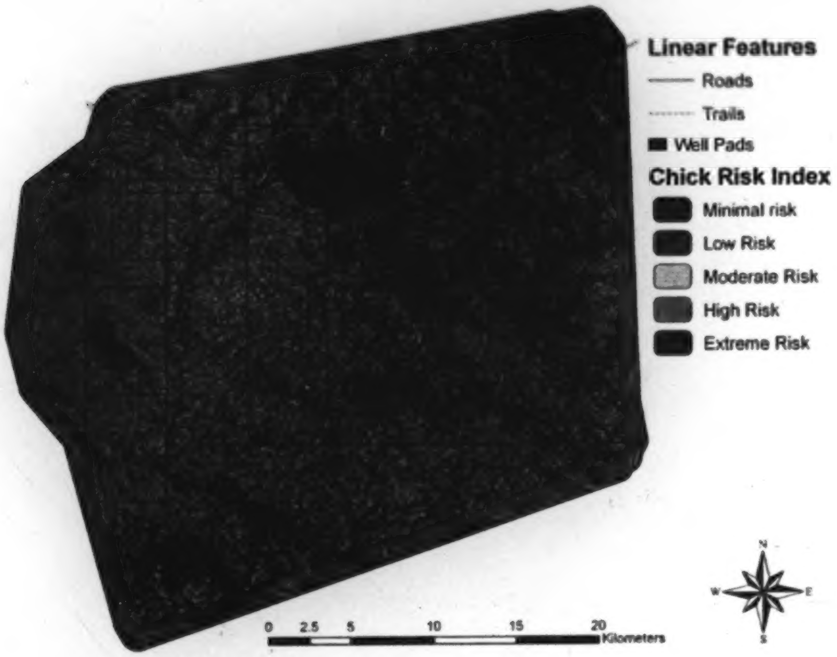
Linear Features
Roads
Trails
Well Pads
Chick Risk Index
Minimal risk
Low Risk
Moderate Risk
High Risk
Extreme Risk
0 2.5 5 10 15 20
Kilometers
N
W
E
S

Figure 4-8. Relative index risk of sage-grouse chick failure in southeastern Alberta, as determined by Cox proportional hazards modelling of chick survival. High and extreme risk values indicated chicks are likely to die if hens move their broods into these habitats.

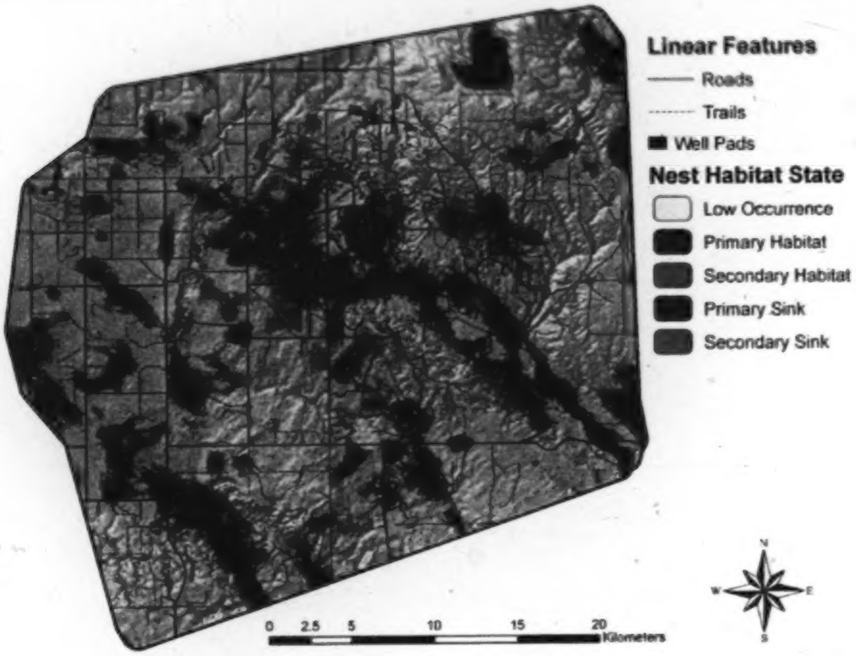
Linear Features
Roads
Trails
Well Pads
Nest Habitat State
Low Occurrence
Primary Habitat
Secondary Habitat
Primary Sink
Secondary Sink
0
2.5
5
10
15
20
Kilometers
N
W
E
S

Figure 4-9. Nesting habitat states for sage-grouse in southeastern Alberta. Non-critical habitat indicates sage-grouse are not likely to nest in those areas. Primary and secondary indicate high and good likelihood of nest occurrence, respectively, and habitats are areas with minimal-low risk of nest failure, whereas sinks are areas with moderate-extreme risk. For example, primary habitat indicates areas where nests are likely to occur (high occurrence values) and be successful (minimal-low risk values), whereas primary sink indicates high occurrence where nests are likely to fail (moderate-extreme risk values).

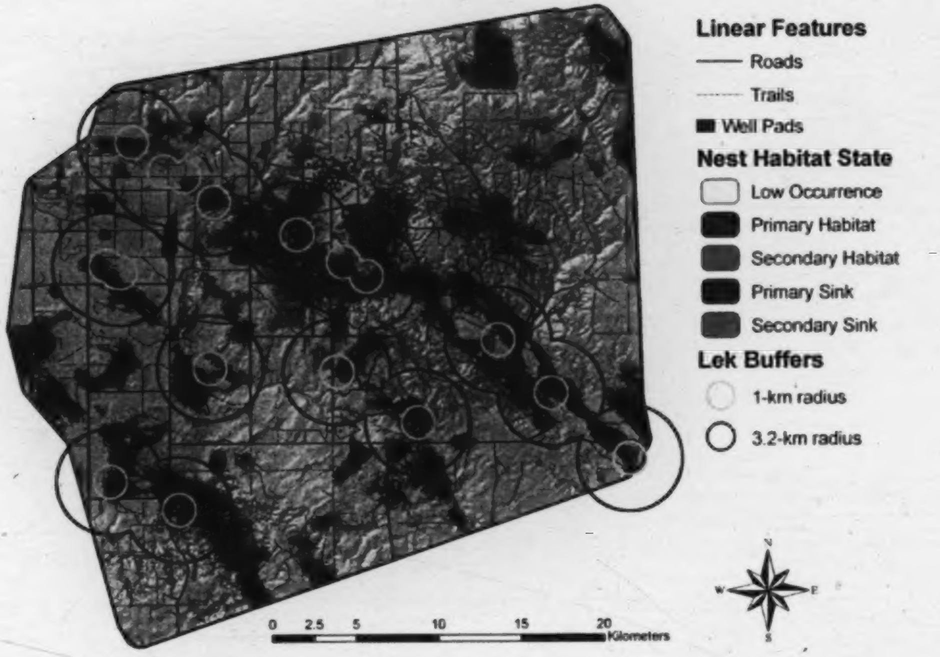
Linear Features
Roads
Trails
Well Pads
Nest Habitat State
Low Occurrence
Primary Habitat
Secondary Habitat
Primary Sink
Secondary Sink
Lek Buffers
1-km radius
3.2-km radius
0
2.5
5
10
15
20
Kilometers
N
W
E
S

Figure 4-10. Nest habitat states that would be included if a 3.2-km radius buffer around all known lek sites was used to protect sage-grouse nesting habitat, as outlined by Connelly et al. (2000). The 1-km radius buffer represents current protective notations or recommended guidelines used by the province of Alberta to protect critical sage-grouse nesting habitat. The 3.2-km buffer includes 53.9% of Primary and Secondary nesting habitat, whereas the 1-km buffer protects only 9.9% of critical nesting habitat.

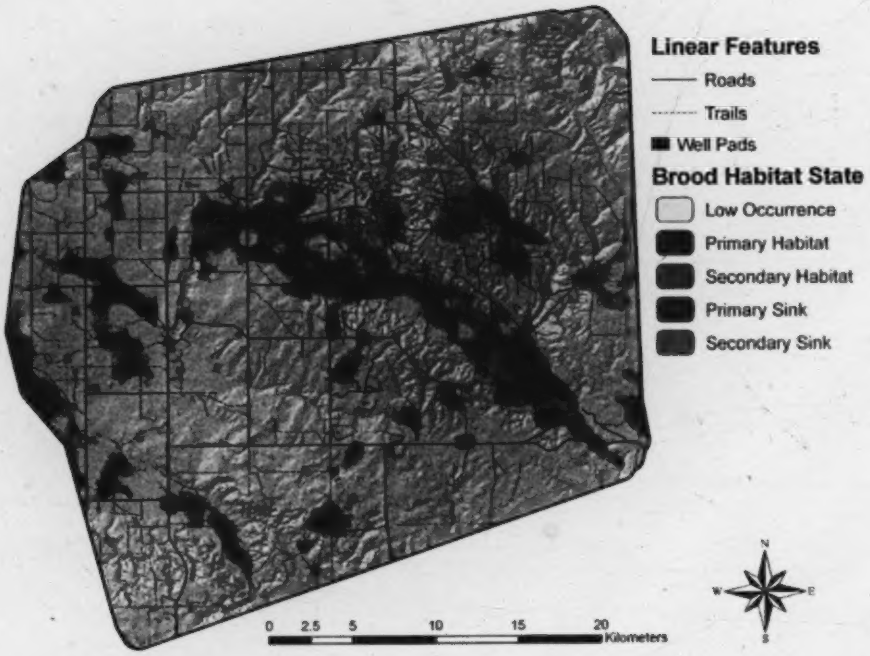
Linear Features
Roads
Trails
Well Pads
Brood Habitat State
Low Occurrence
Primary Habitat
Secondary Habitat
Primary Sink
Secondary Sink
0 2.5 5 10 15 20
Kilometers
N
W
E
S

Figure 4-11. Brood habitat states for sage-grouse in southeastern Alberta. Non-critical habitat indicates sage-grouse are not likely to nest in those areas. Primary and secondary indicate high and good likelihood of brood occurrence, respectively, and habitats are areas with minimal-low risk of chick failure, whereas sinks are areas with moderate-extreme risk. For example, primary habitat indicates areas where broods are likely to occur (high occurrence values) and survive (minimal-low risk values), whereas primary sink indicates high occurrence where chicks are likely to fail (moderate-extreme risk values).

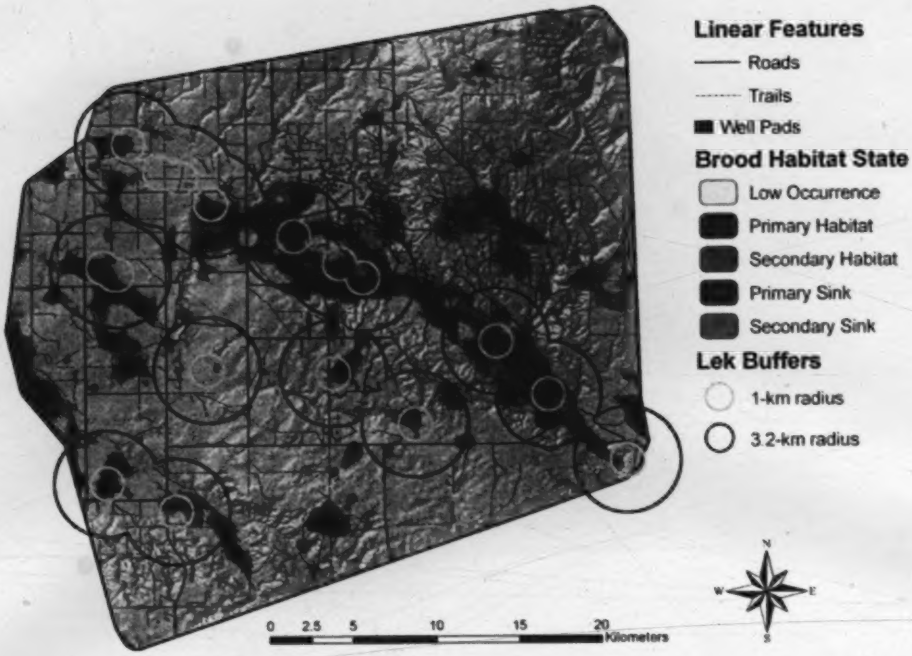
Linear Features
Roads
Trails
Well Pads
Brood Habitat State
Low Occurrence
Primary Habitat
Secondary Habitat
Primary Sink
Secondary Sink
Lek Buffers
1-km radius
3.2-km radius
N
W
E
S
0 2.5 5 10 15 20
Kilometers

Figure 4-12. Brood habitat states that would be included if a 3.2-km radius buffer around all known lek sites was used to protect sage-grouse nesting habitat, as outlined by Connelly et al. (2000). The 1-km radius buffer represents current protective notations or recommended guidelines used by the province of Alberta to protect critical sage-grouse brood-rearing habitat. The 3.2-km buffer includes 62.5% of primary and secondary brood-rearing habitat, whereas the 1-km buffer protects only 9.9% of critical brood habitat.

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Chapter Five

Adaptive Management of Prairie Grouse: How Do We Get There?[1]

1. Introduction

Prairie grouse have been declining throughout North America over the last century (Braun et al. 1994; Braun 1998; Connelly et al. 1998; Applegate et al. 2000a, b). Some of the most marked declines have been recorded for sage-grouse (*Centrocercus* spp.; Braun 1998) and greater prairie-chickens (*Tympanuchus cupido*; Applegate et al. 2000*a*) over the last few decades. Prairie grouse population declines are associated with direct loss of habitat and continued fragmentation and degradation of existing habitat (Braun et al. 1994). Management efforts have been relatively unsuccessful and populations continue to decline. As a result, several species or distinct populations in Canada and the United States have been petitioned or listed as threatened or endangered (Anonymous 2000; Aldridge and Brigham 2003). Too often, managers have taken a 'wait and see' or 'trial and error' approach (Hilborn 1992; Halbert 1993) to managing prairie grouse. This has limited our ability to learn about population regulation and habitat limitations. If appropriately implemented, we believe that adaptive management (Holling 1978; Walters 1986; Walters 1997b) could identify sound management alternatives for prairie grouse populations, advance our learning, and improve management policies to benefit prairie grouse populations. In this paper we present background on the history and idea of adaptive management. We discuss why many adaptive management strategies have failed and illustrate how and why it is important to develop an approach for implementing management policies for prairie grouse within an adaptive framework. We use 2 case studies to illustrate our points: 1 for prairie sharp-tailed grouse (*T. phasianellus*) in Manitoba and 1 for greater sage-grouse (*C. urophasianus*) in Alberta.

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2. History of adaptive management

Buzz Holling, Carl Walters, and Ray Hilborn developed the concept of adaptive management in 1974 through a series of workshops (Ludwig and Walters 2002). The concept was aimed at building models to understand uncertainties associated with natural resources, and involved managers, policy makers, and scientists in the process (Holling 1978; Walters 1986). Walters and Hilborn (1976) introduced the idea of adaptive resource management in 1976. They pointed out that experimentation was the most reliable means of understanding uncertainties in resource systems and comparing alternative models should form the basis of management, experimental design, and monitoring of the resource system (Holling 1978).

The adaptive policy process involves stakeholders and begins by integrating existing knowledge and scientific information into dynamic models used to make predictions about impacts of alternative management practices (Holling 1978; Walters 1986; Walters 1997a). Practices are re-evaluated and adjusted as new information is obtained from current management (Holling 1978; Walters 1986; Walter 1997b). Adaptive management is essentially 'learning by doing' (Haney and Power 1996; Walters 1997b), placed in the framework of experimental design with feedback from the 'learning' stage back into the 'doing' stage. This concept is not new; most managers, scientists, and wildlife biologists are aware of adaptive management. However, it is a poorly understood concept that is difficult to apply or often inappropriately applied (Walters 1997b; Wilhere 2002).

3. Adaptive management definitions and misconceptions

The 2 key components of adaptive management are 1) management is effectively set out as an experiment with a sound experimental design, and 2) a direct feedback loop exists between science and management (Halbert 1993). Essentially, adaptive management is the incorporation of the scientific method (experiments) into a management framework (policy decisions). This differentiates adaptive management from traditional 'trial and error' or 'learn as you go' management (Hilborn 1992; Halbert 1993). Managers and stakeholders involved in conservation planning processes often disregard this and think of adaptive management simply as sound management, or management with a willingness to change (Wilhere 2002). Others see it as flexible management, an opportunity to contest policies they consider objectionable (Wilhere 2002). Bormann et al. (1999:506) defined adaptive management as "an approach to managing natural systems that builds on learning - based on common sense, experience, experimenting, and monitoring - by adjusting practices based on what was learned."

There are various levels at which adaptive management can be implemented, the most simple of which is called reactive management, similar to 'trial and error' management (Hilborn 1992). In this case changes are driven by stimuli external to the management system, such as politics, lawsuits, and public opinion (Bormann et al. 1999). As a result conflicts often arise due to multiple stimuli, resulting in haphazardous management (Bormann et al. 1999; Roe and Van Eeten 2001). Many wildlife management decisions, both old and current, have been made based on reactions, and most resulted in crisis management with 1 policy often trying to correct crises created by earlier management decisions (Bormann et al. 1999; Roe and Van Eeten 2001). Reactive management is unreplicated and lacks statistically valid experimental design, often producing unreliable information (Hurlbert 1984; Wilhere 2002). This often results in implementation of single policies or strategies that are assumed to be suitable without evaluating the policies or comparing alternative strategies or controls.

In contrast to reactive management, passive adaptive management involves long-term monitoring and learning from a gradually evolving management strategy (Walters 1986; Hilborn 1992), but typically lacks scientific rigor (i.e., no replication, no controls, no randomization; Hurlbert 1984; Wilhere 2002). This relatively simple and inexpensive approach involves measuring responses relative to what happened in the past (learning from experience; Roe and Van Eeten 2001), but understanding of causal relationships is limited (Bormann et al. 1999). This process often becomes reactive trial and error management, when funds committed to monitoring are removed (Bormann et al. 1999). Passive adaptive management can be useful in systems that have a high degree of natural variability (Halbert 1993); large enough natural perturbations can be measured and correlated to disturbances. However, if processes other than management are causing the variability (i.e., environmental variability like weather patterns) it can make causal relationships difficult to discern.

Finally, the most rigorous form of adaptive management is active adaptive management (Walters 1986; Hilborn 1992), which occurs through parallel learning (Bormann et al. 1999). This approach differs in that management policies are designed, replicated, and tested against each other. Management is essentially achieved through a series of controlled experiments (Walters 1997b; Bormann et al. 1999; Roe and Van Eeten 2001), identifying cause-and-effect relationships between management activities and changes within the system (Wilhere 2002). This promotes rapid learning and the formation of optimal policies that will guide future management (Wilhere 2002) and prevents the broad application of any single policy that may or may not work, possibly preventing the alteration of future management (Walters 1997b).

The primary difficulty with implementing an active adaptive management strategy is replication, making it difficult to use in a single or unique system (Walters 1986), (e.g., small endangered populations; Boyce 1993). One option may be to implement various management strategies in separate subpopulations (Boyce 1993), possibly comparing treatment effects between areas with similar characteristics. In this case it would be difficult to control for spatial variation, but replication of treatments may be achievable.

Another approach for adaptive management of small populations is the Before-After-Control-Intervention (BACI) design, originally identified by Green (1979). With this design, variability in the system is monitored prior to intervention. In adaptive management applications, the key elements of a BACI design include replication, controls, and monitoring both before and after management intervention. In cases where management policies will take place at the scale of the entire population (i.e., small populations), replication is impossible. However, management actions can be compared using an information–theoretic approach. By framing treatments in the context of multiple working hypotheses (Chamberlin 1890; Anderson et al. 2000), hypotheses would consist of a series of *a priori* candidate models; management options outlined during policy planning meetings (Walters 1997b, see below). If a particular strategy achieved a biologically meaningful goal (Reed and Blaustein 1995), such as an increase in population size of a predefined magnitude, then the strategy should be considered successful, regardless of the statistical significance of the experiment. With this comparative approach, the adaptive management process is still used, and biological goals can be tested.

4. Reasons adaptive management fails

Adaptive management can fail for a variety of reasons (Walters 1997a; Moir and Block 2001). The major flaw is that the process rarely progresses from the model development stage to the design and implementation of field experiments. Walters (1997a) participated in 25 adaptive management planning processes with only 7 (28%) resulting in large-scale management experiments; 2 (8%) of which had well-planned experimental designs with controls and suitable replication. Walters (1997a) suggests experiments often are opposed by people protecting self-interests in management bureaucracies and that proponents of adaptive management need to be forceful and expose these groups and their interests to public scrutiny. This will help to keep the adaptive management process on track and maintain the sustainability of public resources. Value conflicts arise from the necessity of involving all stakeholder groups with an interest in the resource in the decision-making process, each potentially possessing different values, morals, and opinions (Walters 1997a).

Adaptive management needs effective implementation of experiments, which may be expensive or risk prone (Macnab 1983; Halbert 1993; Walters and Green 1997;

Walters 1997a) compared with baseline options, especially when threatened or endangered species are involved. Public agencies by nature are risk-averse and manage for the status quo (Halbert 1993). However, if risk-averse status quo management (Halbert 1993) is not benefiting a threatened species, then adaptive management presents a viable option. Identifying uncertainties early in the planning stages (see below) will eliminate individual or multiple management options that may pose risks (Walters 1997b).

Even if experimental designs are implemented, adaptive management often fails because the information feedback loop (monitoring and evaluation) is broken (Moir and Block 2001). Thus, learning is inhibited and there is no evolution of management policies. This loop typically is broken as managers are looking (by necessity) for short-term responses and feedback from management policies (Moir and Block 2001). However, the realization that responses to management may be longer term needs to be identified by stakeholders during initial policy planning to avoid such conflicts.

Below, we present 2 case studies in which attempts were made to implement adaptive management strategies for prairie grouse. Both attempts failed to successfully implement adaptive management; however, we feel there are important lessons to be learned from our experiences.

5. Case Study 1: Manitoba sharp-tailed grouse

In Manitoba a pilot project for sharp-tailed grouse habitat management using principles of adaptive management has been underway for a number of years. The program is a partnership approach, including a local nonprofit organization, the

Sharptails Plus Foundation, in association with the University of Manitoba and the Manitoba Department of Conservation.

Population estimates for sharp-tailed grouse in Manitoba indicated a decreasing population, although they are still at relatively high levels when compared to other North American populations (Froese 2002). Habitat alteration was suggested as the cause of the long-term decline (Baydack 1996). In more southerly areas of the province, agriculture had eliminated historically important cover types, particularly shrubland and woodland; whereas, in central areas, fire suppression and reduced grazing had caused shrubland and woodland to increase above historic levels (Berger and Baydack 1993). In central areas such as Manitoba's Interlake region, sharptails were thought to have thrived historically in diverse vegetative cover, roughly equivalent to an equal one third mix of grassland, shrubland, and woodland (Bird 1961). This historical composition has changed throughout the province, most notably with respect to shrubland composition, which is nonexistent in many areas (Berger and Baydack 1993).

To address the effects of habitat alterations on sharp-tailed grouse populations, a private, nonprofit organization, the Sharptails Plus Foundation, was created in Manitoba in the early 1990s. The organization is volunteer-based, comprised of relatively influential citizens whose overall goal has been to enhance the habitat condition for sharp-tailed grouse and, thereby, influence population levels throughout the province. Although the primary focus of the organization is on sharp-tailed grouse, members recognize their work will affect many other species and communities, hence the 'Plus' designation in their name. In the early 1990s, Sharptails Plus began to implement a variety of habitat-related programs across Manitoba with the help of a Technical

Advisory Committee of ecologists, agrologists, and land managers. Their Private Lands and Pilot Projects Program was developed with the intent that it be implemented using concepts of adaptive management.

The program was created on the basis of several important underlying concepts. Cooperation with agriculture was essential for effective sharp-tailed grouse habitat management to be achieved. Landowners were seen to have reasons for doing what they do, and they are, in effect, the real habitat managers in much of Manitoba. Sharptails Plus recognized that understanding the motivation for landowner decisions respecting habitat and wildlife on their property was important. Similarly, Sharptails Plus recognized that data generally were lacking from a biological perspective about how to 'best' manage a parcel of land to meet sharp-tailed grouse needs. Finally, landowners needed to continue to 'manage' their holdings, regardless of whether the 'final' biological answer could be provided. The Technical Advisory Committee of Sharptails Plus noted that this created an opportunity for implementation of an adaptive management program that utilized the best available local knowledge from landowners and biologists to reach management prescriptions that could be tested against each other. Steps in the Sharptails Plus (STP) Foundation Private Lands Program included the following:

1. Interested landowners in target locations were identified.
2. STP Technical Advisory Committee (biologists, agrologists, land managers) assessed existing habitat along with individual landowners.
3. Habitat objectives were established for each location in consultation with landowners, generally based on the percent cover of woodland, shrubland, grassland, and cropland, compared to the historic one third levels.

4. Independently, the STP Technical Team and landowners developed their own habitat-management treatment recommendations for each location based on their individual reasoning.
5. Land parcels were randomly allocated to each 'competing' management option resulting in an overall 'Adaptive Farm Management Plan.'
6. Management treatments were monitored, evaluated, and refined annually using both biological and economic measures. Budgetary constraints prevented radio-marking grouse to track their response to changing vegetation over time and limited monitoring to attempts to locate sharp-tailed grouse leks and nest sites. If leks were located near treatment sites, at least 5 counts of sharptail abundance were recorded annually in spring within 0.5 hr of sunrise, and these counts were compared over time and among treatments. Vegetative measurements were taken before and after treatments in spring, summer, and fall at every treatment site, using a nested block design as described in Froese (2002). Measurements were dependent on the treatment applied and included vegetation composition, structure, height, rate of growth, percent kill of unwanted species, and others. Economic analyses of treatments also were performed annually and compared over time (Froese 2002).

A variety of management treatment options were available for consideration at every management location, including: rotational and pulse grazing, delayed mowing and haying, leaving increased edge, planting shelterbelts and woodlots, prescribed burning, mechanical removal of vegetation, chemical removal of vegetation, and food quadrats.

The Program has been operational in Manitoba at 4 locations (near the communities of Plumas, Lundar, Chatfield, and Vita) for the past 5 years. Preliminary results revealed the following trends:

- Landowners seem generally satisfied with the outcomes which have resulted in increased forage use for their cattle and an apparent increase in sharp-tailed grouse abundance, although increased monitoring (i.e., daily or twice daily) of activity on leks in spring and or use of radio-marking has been suggested.
- Most landowners considered indicators of 'success' to be whether a sharp-tailed grouse lek was actually established on their properties, often a difficult expectation to achieve.
- Biological indicators of success related to attainment of desired cover composition (% cover in woodland, shrubland, grassland, cropland), which generally has been possible.
- Management treatment options proposed by biologists were no better in achieving vegetative cover composition 'success' than those suggested by landowners.
- Monitoring of economic indicators suggested that incentive programs would be necessary to offset increased costs to farm operations. However, estimated costs of treatments likely were higher than would be expected due to the cost of smaller-scale experimental procedures used to formulate estimates.

On the basis of the success of the program to date as perceived by landowners, the Sharptails Plus Foundation (Adaptive) Private Lands and Pilot Projects Program will continue in Manitoba into the foreseeable future. Although the Foundation is finding that financial requirements continue to be relatively high compared to their available resources, they believe the Program is useful to ensure local support for conservation measures and to increase the area of coverage within the province. The program is recognizing that dedicated landowners are the real key to success for managing sharp-tailed grouse on private lands in Manitoba, and perhaps more importantly, that dedicated landowners are at least as successful as biological managers in knowing the best practices for their landholdings. Therefore, a pressing need exists to encourage the 'release' of this valuable local knowledge onto the prairie landscape so as to enhance management of wildlife habitats for future generations.

This case study represents a good initial attempt at managing declining sharp-tailed grouse numbers and was successful in achieving some of its goals. The program began using a collaborative planning process (Walters 1997b) and set out to improve habitat for sharp-tailed grouse by creating habitats similar to historical times when sharp-tailed grouse were more abundant, with an equal one third mix of woodland, shrubland, and grassland. Most management techniques appeared to be successful at achieving vegetation goals; however, the process was limited from the beginning, when funds for grouse evaluations could not be allocated. Realistically, evaluation of the program should be judged by how successful it was at creating habitats beneficial to, and used by the birds, hence increasing population numbers. In addition, other measures of biodiversity could have been incorporated into the monitoring programs so as to provide additional indicators of success for management decision-making.

6. Case Study 2: Implementation failures of Alberta sage-grouse adaptive management

The greater sage-grouse in Alberta has experienced some of the highest rates of decline of any known sage-grouse population (66–92 % over the last 30 years; Aldridge and Brigham 2001; 2003), and the species is listed as endangered at both the provincial and federal levels. Research completed in 1999 suggested that limited residual cover and litter build-up was limiting the population through poor chick survival and low nest success (Aldridge and Brigham 2001; 2002). To document the role of range management, it was recommended that a variety of stocking rates be used in 2000-2001 in an attempt to enhance litter build up and residual cover for sage-grouse and that the response of the vegetation and sage-grouse be monitored.

The goal of this management experiment was to assess the effect of grazing on nesting success of sage-grouse. We (C.L.A. and M.S.B.) designed the experiment with replicate treatments using 3 stocking rates, (all various levels lower than current rates) and had many sites that maintained current stocking rates (controls). We chose sites (treatments and controls) with similar grazing histories; previous stocking rates, season and duration of grazing. Treatments were randomly allocated (bounded by landowner participation) and replicated over different pastures, allowing us to compare management treatments (stocking rates) against each other and controls. Individual nest sites located within each treatment unit (pasture) would be grouped and the size of the treatments and controls kept similar, albeit limited to the size of currently utilized pastures. However the effect of treatment size also could have been incorporated into the experimental design to test for an effect of treatment size (see step 4 below). A nested design was used to avoid pseudoreplication (Hulbert 1984) with each additional nest site within a treatment increasing our power to detect differences. Below, we highlight why this approach has failed, then describe how the process still may be implemented by adopting a collaborative adaptive process (Walters 1997b).

In spring of 2000, with fears in the ranching community about the pending Canadian Species At Risk Act (SARA) and its potential consequences for management, scientists suggested that Alberta Sustainable Resource Development (SRD) and the Canadian Wildlife Service (CWS) hold public forums with local ranchers. The 2 organizations were to work under the umbrella of the CWS Endangered Species Habitat Stewardship program to approach landowners who might be interested in participating in adaptive sage-grouse range management experiments. Due to a lack of funds from government agencies in summer 2000 and the sensitive and political nature associated with the pending endangered species legislation, this uncoordinated approach failed and only added to local landowner concerns about outsiders attempting to manage their land.

In 2001 SRD collaborated with the Alberta Conservation Association (ACA) to develop management strategies. However, at this point there was no involvement of Alberta Public Lands, the agency charged with managing the public lands that constitute > 80% of current sage-grouse habitat in southern Alberta. The ACA had a habitat management program, the Native Prairie Stewardship program, expanding into the area, providing opportunity for collaboration. The program's focus was on developing and implementing sound range management to improve residual cover and litter for wildlife (important for nest success and chick survival of both sage-grouse and sharp-tailed grouse). The program worked with individual ranchers to develop range management plans for each participating ranch and then helped to focus new management initiatives, assisting landowners with cost of implementation.

This program had limited monitoring and evaluation components, both important parts of the initial design process, as well as management policies themselves. As the program continued into 2003 under the premise of 'enhancing' and 'protecting' critical habitat for both sage-grouse and sharp-tailed grouse, some post-hoc song bird counts were added in an attempt to evaluate the effectiveness of the program. However, without suitable evaluations, there is no way to ensure the management initiatives achieve desired ecological goals.

At roughly the same time, the Nature Conservancy of Canada (NCC) began signing conservation easements in the area and developing management plans with the notion of protecting sage-grouse habitat. Like the Native Prairie Stewardship program, there is limited evaluation associated with the NCC program. Both programs develop conservation management plans that are private landowner agreements, not allowing others access to the management plan or actions. By creating independent ranch management plans void of experimental treatments and preventing access to management policies, currently radio-marked sage-grouse on these ranches could not be used to understand how grouse respond to management initiatives, preventing an adaptive approach involving evaluation and subsequent evolution of management strategies.

As a result of these activities and proposed management, Alberta Public Lands also became involved in sage-grouse management. They began their own initiatives to address the decline of sage-grouse, unconvinced that grazing was related to sage-grouse declines. This resulted in 5 different agencies developing management strategies for sage-grouse and effectively overwhelming landowners with sage-grouse issues, causing them to close their doors to ongoing research. As a result, SRD coordinated a public meeting with landowners, researchers, and Public Lands in spring 2002. This resulted in the formation of a Provincial Recovery Action Group (RAG) designed to bring together science, management, industry, and landowners in a collaborative effort aimed at implementing adaptive management strategies for the recovery of sage-grouse in Alberta. Walters (1997b) suggests this is the first step involved in the policy-planning process necessary for the successful implementation of adaptive management (see summary below). This process will incorporate evolving economic and social concerns, as well new biological information pertaining to the system, an important process in adaptive management (Haney and Power 1996).

Delays in implementation continued, as Alberta Public Lands refused to embrace the uncertainty about grazing, insisting there was not enough information to begin adaptive trials. Adaptive management should embrace this uncertainty, allowing for further understanding of the system through the implementation of a series of sound experimental management policies. However, Public Lands undertook their own research, including background range inventories, developing a sagebrush soils classification, performing water impediments studies, and performing a historical grazing practices study. While retrospective studies may provide some insights, management experiments were postponed. Walters (1997b) points out that if policy-design processes begin by attempting to identify all scientific uncertainties about a system, then that process will fail on the simple fact that there is an infinite number of uncertainties. The goal of adaptive management is to embrace these uncertainties through experiments, increasing our ability to learn about the system.

The RAG is now showing signs of progress. After appointing a moderator familiar with the adaptive management process in late 2002, the group is approaching management following methods similar to Walters' (1997b) policy planning process, albeit 3–4 years after the initial investment of funds by 5 different agencies and stakeholders. The RAG was able to bring together industry and conservation representatives, as well as managers, scientists, and landowners for the planning process. Representatives and the organizations they represent have all bought into the process, most committing long-term to the RAG. Currently, the group is developing models to predict the outcomes of certain policies and management options, aimed at identifying and understanding uncertainties within the system (see steps 2 and 3 below). While adaptive management most often fails prior to implementing experiments (Walters 1997a), by following an adaptive policy design process similar to that outlined by Walters (1997b; see below), the RAG will be able to identify sound management options and will have the opportunity to implement those management options as a series of experiments with suitable monitoring and evaluation components.

These 2 previous prairie grouse examples illustrate how important it is to have local involvement and 'buy-in' at the policy-planning stages of adaptive management (Freyfogle 1998) and how easily the process can fail without it. Below, we discuss how one might implement a successful adaptive management policy and avoid the same mistakes we encountered during the policy-planning stages, prior to implementing any management experiments.

7. Implementation of successful adaptive management

The implementation of an adaptive management policy begins with stakeholder gatherings and identification of all elements, variables of interest, management acts, objectives, indicators, time horizons and spatial extents (Holling 1978). This is often 1 of the most difficult steps to undertake, but a concerted effort to involve all stakeholders at the beginning of the process will reduce the chances of failing at later stages and provide a sense of ownership to the decisions for each group involved. Ensuring that conservation groups, local landowners, industrial representatives, and managers stay committed to adaptive management processes over the long term can be difficult, especially given the turnover of individuals within most agencies and the fact that local landowners have limited time to commit to such efforts. This is where having an independent facilitator familiar with adaptive management and policy planning can reduce the length of the process and time commitments. This moderator needs to be meticulous in recording details of process developments, obtaining commitments from agencies and organizations at the beginning of the process. Timelines for implementation of management strategies, including monitoring, evaluation, review of the adaptive process, and commitment of funds from groups involved, must be identified and outlined upfront in management or conservation plans being developed. This will provide structure to the adaptive management process and ensure long-term involvement of individuals and commitment of financial resources from each group, even when personnel changes occur. We believe that if individuals and organizations involved with managing prairie grouse populations adopted similar methods, learning about prairie grouse populations would be advanced and habitat management problems could be addressed more effectively.

Once stakeholders come together, the first step is to define policy options and identify policy performance measures (Walters 1997b). This is where management options are identified and uncertainties about those outcomes and consequences are outlined. These options can vary over space and time, thus, it is useful to define a ballpark scale for treatment comparisons. If management is directed at a single species, one must consider the scale(s) at which the species is likely to respond to the management. For example, if one implemented cattle exclosures to enhance prairie grouse nesting habitats, careful consideration must be given to the size of patch managed which may elicit responses by grouse. Implementing grazing practices can be difficult at scales other than those at which pastures are typically managed. Thus, one must think about the scale at which management occurs, as well as the scale at which a biologically meaningful response is likely to occur. The goal of adaptive management should be to seek out untested options and to evaluate new methods, not to find a cookbook best-prescription. Policy planning should include performance measures for each strategic option (Walters 1997b). This likely will include measures such as economic costs and benefits, ease of implementation, likelihood of success, and others, as well as the original biological goals (Walters 1997b).

The second step in the policy-planning stage is to identify major uncertainties by trying to predict the outcomes to policy alternatives (Walters 1997b). The candidate set of policy options identified in the first step is used to generate models and simulations to predict each policy's impact on desired performance measures (Walters 1997b). These predictions should not be considered as simple static comparisons; they need to be temporal predictions, as uncertainties in the importance of time scales will inevitably arise (Walters 1997b). This process should remove policies not directly relevant to the questions at hand and those likely to fail to begin with. In the sage-grouse case study, the Native Prairie Stewardship Program attempted to improve range habitat conditions for livestock (and wildlife) by creating several watering sources in upland habitats to more evenly distribute cattle. While this might reduce grazing impacts in important mesic sage-grouse brood-rearing habitats, increasing cattle activities in upland areas could negatively affect nesting success for sage-grouse. Thus, this management strategy would likely be identified early during the planning process as problematic and be modified or abandoned all together.

The third step in Walters' (1997b) process involves screening of models to define a good set of policy treatments. This is the process of weeding out policies that are not worth testing because they may have hidden pitfalls or deleterious cumulative impacts that would prevent the achievement of management goals. The modeling processes identified in step 2 will help to identify these hidden pitfalls.

Step 4 involves partitioning the landscape into experimental units at scales appropriate to the uncertainties (Walters 1997b). Walters suggests 2 questions that should be posed at this stage: 1) What portion of the land should be devoted to each of the basic treatment regimes? and 2) How large should each experimental unit be? This is also the stage where uncertainties about the size of experimental treatments can be tested and included as an experimental unit. For our sage-grouse grazing-intensity example, we proposed to implement several treatments with different levels of grazing pressure for comparison. Concurrently, or as an independent experiment, tests for the optimal treatment patch size could be conducted. The amount of replication would depend on the size of experimental units, potentially limiting the number of management policies that could be tested. With an endangered prairie grouse population, the population could be divided into an experimental unit and a control. However, this is where implementing the BACI design (Green 1979) may also be useful.

Next, the temporal and spatial scales at which key responses should be monitored must be considered (Walters 1997*b*). This is where science and management often are in direct conflict, but when they should be in harmony (Johnson et al. 1997). The priority should be to develop a sound and replicated experimental design that, as directly as possible, addresses the question(s) at hand. One must also remember that the time scale is an issue and answers to management questions may not be available immediately after implementation. This is where long-term commitments of individuals, organizations and funds, as identified early in the planning stages, can ensure the successful identification and, thus, implementation of adaptive management.

Walters (1997*b*) encourages the use of Adaptive Environmental Assessment Modeling (AEAM; Holling 1978; Walters 1986) as the sixth and final step in his policy-planning process. AEAM is a stakeholder involved evaluation process that uses simulation modeling to predict future conditions (Holling 1978; Walters 1986). Maintaining the involvement of a wide range of stakeholders gives each of them 'ownership' in the plan and strengthens the adaptive management process.

For both of the prairie grouse case studies we presented, attempts to implement sound adaptive management experiments failed. This is not uncommon. Most attempts to implement adaptive management in a variety of different systems tend to fail in the planning stages, prior to implementing experiments (Walters 1997b). However, by following the policy-planning steps we have presented, common mistakes in the planning stages can be avoided, the most appropriate management policies meeting biological, economic, social, and political goals can be identified, advancing the adaptive management process to the experimental phase, where management policies are implemented. By definition, adaptive management is an evolving process. To complete the full adaptive cycle, management strategies must be evaluated following the monitoring strategies outlined in the planning process. As new understandings occur, management strategies need to evolve and incorporate new information.

8. Conclusions

To our knowledge, experimental adaptive management has yet to be successfully used as a tool to advance learning and management of prairie grouse populations. More broadly, adaptive management seldom is successful with about 75% of policy-planning processes failing to implement adaptive management as experiments and less than 10% possessing sound experimental design with suitable replication and controls (Walters 1997a*)*. Although adaptive management has become a popular idea among management agencies and can be useful when implemented correctly, in practice, adaptive management often is used as a buzzword and never implemented. Ludwig and Walters (2002) suggest this may be a defensive measure by bureaucrats attempting to demonstrate that change is occurring without actually changing anything. Adaptive management sets out to embrace uncertainties associated within a particular system, resulting in an increased understanding of the system by managing through experiments (Holling 1978;

Halbert 1993). This allows for appropriate 'common sense' policy decisions to be identified (Ludwig and Walters 2002).

Adaptive management can be expensive, but balances have to be achieved between contributing available funds towards habitat protection and allocating funds for adaptive management (Wilhere 2002). For adaptive management to succeed, there must be a commitment to long-term monitoring and evaluation that promotes learning and feedback into management strategies. Walters and Green (1997) suggest that approximately 20% of funds allocated to any management plan need to be set aside for monitoring and evaluation. Unfortunately, most habitat conservation plans lack sufficient monitoring to evaluate the success of the plan (only about 5% of plans created in 1999 had a suitable monitoring component, [Kareiva et al. 1999]). Large government conservation initiatives typically do not promote the inclusion of monitoring in management plans. For instance; in 2000 the Canadian Wildlife Service implemented a 5-year, 45 million-dollar Habitat Stewardship Program aimed at protecting at-risk species and their habitats through conservation actions. However, guidelines for the program prohibit the use of the funds for the evaluation of the strategies. The importance of monitoring and evaluation in management is frequently misunderstood and failure to document consequences of management often results in the failure of many adaptive management plans. The most successful information technology companies in the world (XEROX, Kodak, IBM, and AT&T) recognize the importance of research and development, typically reinvesting about 10% of corporate earnings back into research and development (Gill 1997).

The management of prairie grouse needs to adopt an adaptive framework, and we recommend using Walter's (1997b) adaptive policy-planning process as a guideline to ensure that the process does not fail in the planning stages and that sound management options are identified. This process will enhance the probability of sound management experiments being implemented with suitable monitoring and evaluation components. Both case studies we presented on prairie grouse are excellent examples of how lack of a coordinated effort will cause implementation of independent and possibly harmful, management policies that lack scientific rigor and appropriate monitoring and evaluation components. However, the Alberta sage-grouse example also shows that following an adaptive policy planning process (the RAG), the most common problems stalling the adaptive process (involving stakeholders, identifying and implementing sound experimental policies) can be avoided, and allow policy alternatives to be modeled and compared, identifying uncertainties. This process will allow management to be implemented as sound scientific experiments, the goal of adaptive management.

Conservation plans developed by a group of stakeholders to identify management priorities have been undertaken for many prairie grouse populations (C.E. Braun, Grouse Inc., personal communication); an important initial step in the adaptive management process. However, like most habitat conservation plans, prairie grouse conservation plans typically lack suitable monitoring and evaluation programs. Even if conservation working groups successfully identify and implement conservation actions, uncoordinated implementation of actions has made it impossible to identify appropriate methodologies to assess impacts on population numbers, as has been the case with the Gunnison sage-grouse conservation plan (Anonymous 1997). Structuring management policies as adaptive experiments should be a priority for individuals and organizations managing prairie grouse populations.

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Chapter Six

Thesis Synopsis

There is no doubt that greater sage-grouse (*Centrocercus urophasianus*) populations have experienced drastic declines (Connelly et al. 2004), and some populations are threatened with local extirpation. The Alberta population has experienced the most drastic reduction in range size, as well as population numbers (Aldridge and Brigham 2003). This population continues to decline under 'status quo' management. Predictions suggest that the population will fall below 100 individuals by 2020, which may not be enough to ensure its viability (Aldridge 2001). Similar to other struggling sage-grouse populations (Connelly et al. 2004; Crawford et al. 2004), the decline in Alberta is a result of low recruitment due to low nest success and poor chick survival (Aldridge 2001; Aldridge and Brigham 2001). Ensuring high-quality habitats remain functional (high occurrence and high fitness; Van Horne 1983; Morrison 2001) for these critical life stages will ensure that the Alberta sage-grouse population remains viable.

In Chapter 4, I used landscape scale models to identify and map primary and secondary source nest and brood habitats for sage-grouse in Alberta. These habitats must be protected from further anthropogenic threats, such as cultivation of native prairie, development of human structures, and oil and gas activities, all of which I show are either avoided or have negative fitness consequences for either sage-grouse nests, chicks, or both. Care should be taken to prevent road and electrical line developments in these areas, which have been shown to have negative consequences for other prairie grouse species (Hagen 2003; Pitman 2003). Sound range management practices within these areas will maintain critical nesting and brood rearing habitat. As identified in chapters 2 and 3, local escape cover provided by sagebrush, grass and forbs, and suitable food resources (sagebrush and forbs) must be managed to meet or exceed thresholds. In addition, my landscape scale models identified that sage-grouse are unsuccessful in many of the habitats they choose to occur, resulting in ecological traps (Delibes et al. 2001; Battin 2004). These areas need to be actively managed in order to improve nest success and chick survival. In these regions, reclamation and removal of roads, and the coordinated 'sharing' of roads between energy companies operating in the area has the potential to greatly improve habitat quality. Capping power poles or burying existing power lines could reduce the number of perch sites for raptors that prey upon sage-grouse. Removal of some existing drilling wells and reclamation of well pads may be necessary to reduce the risk of chick failure in these habitats.

Local management of cover and food resources also will be necessary in these habitats, using the thresholds I described above and in Chapter 2 and 3 as guides. Indeed, the expertise of provincial range agrologists and the range science community will be required to identify approaches that are most likely to achieve these desired goals, possibly using grazing as a tool to improve habitats for sage-grouse. Unfortunately, as I identify in chapter 5, our understanding of the role of grazing in achieving these desired targets is poorly understood. This highlights the need to adopt a collaborative adaptive management approach (Aldridge et al. 2004) when attempting to enhance local (or landscape) vegetation characteristics for the benefit of sage-grouse, and other wildlife species. If enhancements are treated as experiments, range mangers will gain a better understanding of how to best meet required sage-grouse thresholds for vegetation cover and structure. If conducted with continued radiotelemetry studies, which allow for the monitoring of sage-grouse habitat selection and fitness, wildlife managers will be able to appropriately evaluate the role of grazing on sage-grouse population dynamics; a primary management requirement for the species range wide (Crawford et al. 2004).

Within Alberta, protection of lek sites under the province's setback guidelines (suggested distances for which limited petroleum industry activities should take place to protect sensitive wildlife species; Scobie and Faminow 2000), protective notations on lek sites were implemented, restricting enthusiastic naturalists and conservationists from observing (and 'disturbing') the unique mating rituals of sage-grouse. Although some individuals disrupt mating activities by flushing birds off of the lek sites, most people are respectful and appreciative of our great wildlife resources. With the closing of the hunting season in 1995 (Aldridge and Brigham 2003), and inability for people to observe sage-grouse in their native habitats, the greater public knowledge and awareness about the dire situation sage-grouse are in is all but non-existent, lowering conservation interests. In effect, sage-grouse have been put in a black box, which may be a coffin for the species in Alberta. If appropriate management actions are not implemented to reverse the population decline, sage-grouse will likely disappear from Alberta within 20 years (Aldridge 2001). This thesis provides managers with some tools that should help to prevent this dire situation and begin to manage habitat with the potential to ensure the long-term viability of sage-grouse in Alberta. However, in a province with priorities of economic development and resource extraction, the tradeoffs will have to be made clear and desire from the public to save the sage-grouse will have to be strong enough to outweigh the political powers. In the words of the father of wildlife conservation, Aldo Leopold, “A rare bird or flower need remain no rarer than the people willing to venture their skill at building it a habitat” (Leopold 1933). If there is a will, I think I have outlined a way.

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